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## Muscles of the Pelvic Limb in Galliform Birds

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## INTRODUCTION

Although some of the appendicular muscles have been studied in a few gallinaceous birds by various investigators, no one has made a systematic attempt to work out in detail the similarities and differences between representatives of the various genera and families. Our study of examples of 25 genera is only a short step toward obtaining an over-all picture of the myology of the pelvic limb in this order. The greatest handicap to such a study is the extreme difficulty of obtaining adequate material, especially of types found only in remote parts of the world.

Perrin (1876), the first to undertake a comprehensive study of the wing, leg, and tail myology of *Opisthocomus*, included an extensive section on the muscles of the pelvic limb. He did not make any comparisons with the gallinaceous birds but referred to certain similarities between *Opisthocomus* and the barn owl, considering these analogous. He further mentioned similarities between *Opisthocomus* and the wood pigeon.

Garrod (1879:112) mentioned certain muscles of both limbs in his paper on *Opisthocomus*. He pointed out that the slender tendon of the ambiens disappears in the knee region, although he found it joining the perforated flexors in one case out of six.

The monograph of Gadow and Selenka (1891) remains the most comprehensive work available on the comparative myology of birds. They reported the absence of the Pars caudifemoralis of the piriformis in *Meleagris* and *Pavo* (p. 159). Our observations differ from their descriptions in the following respects: We find the Pars caudifemoralis of the piriformis greatly reduced but not absent in *Pavo*; they reported (p. 183) the peroneus profundus (peroneus brevis) as lacking in *Penelope* and *Gallus bankiva*, although we found this muscle present in all specimens of gallinaceous birds examined.

Flynn (1909) in discussing the anatomy of Megapodes gave general descriptions of many of the leg muscles but these are not sufficient to use in detailed comparisons.

Kopperi (1928) included five genera of Galliformes in his comparative study of the toe muscles of birds. He described in *Gallus* (p. 219 and Fig. V, 1) a separate Ext. brev. d. III which from our dissections we believe to be the Ext. pro. d. III; the structure he labeled "ext. pr. dig. III" we consider a sheet of connective tissue and/or nerves and blood vessels. He did not find the flexor brevis digiti III (lumbricalis) in *Bonasa* (p. 230), although we found this present but weak in all gallinaceous birds with the possible exception of *Pavo*.

Hudson (1937) worked out the muscles of the pelvic limb in *Pedioecetes* and *Colinus*. His observations are in agreement with most of our findings based on a larger sample. However, we do not agree entirely with the description (p. 68) regarding which tendons pass through bony canals in the hypotarsus. Our findings furthermore do not agree with the statement (p. 69) that the obturator internus is



typical in *Pedioecetes*, since we find a very weak portion of origin from the ventrolateral surface of the ilium. We cannot find any distinct difference in the origin of the F. dig. I. in *Pedioecetes* and *Colinus*. Our observations confirm the absence of the Add. d. II in *Pedioecetes* and, for that matter, in all Tetraonidae studied.

Ridgway and Friedmann (1946:2) gave the myological formula of Galliformes as ABXY+, stating that the femorocaudal muscle is absent in *Pavo* and *Meleagris* and very slender in the Cracidae. We found it to be present, but without connection with the tail in *Pavo*; it was narrow in *Crax*, less so in *Pipile*, and fairly wide (more than  $\frac{1}{2}$  the width of the P. il. fem.) in *Penelope* and *Ortalis*.

Berger (1955) commented briefly on some thigh and shank muscles of *Crax nigra*. Among other things he reported the presence of a complete myological formula, the calcification of many tendons, the presence of the Il. troc. med. as a separate muscle and the presence of a large component of the Obt. int. arising inside the pelvis.

The muscle terminology used in the present paper follows that of Hudson (1937). Fisher and Goodman (1955) employ a different set of names for many muscles of the thigh.

*Acknowledgments.* — We are very grateful to those who made this study possible by generously contributing specimens for dissection or assisting in other ways. Dr. Herbert Friedmann loaned several birds from the collection of the U. S. National Museum. At the State College of Washington Dr. Herbert L. Eastlick supplied several specimens of the silky fowl; Dr. Irven O. Buss, a European partridge and Franklin's grouse; Clarence Nagra, a ring-necked pheasant; John V. Spencer, numerous chicken and turkey specimens; Jared Verner, a Franklin's grouse; Dr. Donald S. Farner made helpful suggestions concerning the acquisition of Megapodes. Members of the Washington State Department of Game donated specimens as follows: Henry A. Hansen, a sage grouse and two guineas; L. D. Parsons, a sharp-tailed grouse; James C. Stout, a sage grouse; Carl V. Swanson, two bobwhite quails; Fred Zwickel, a sharp-tailed grouse. Through the efforts of Thomas D. Burleigh of the U. S. Fish and Wildlife Service, a prairie chicken was contributed by Dr. Frederick Hamerstrom of the Wisconsin Conservation Department. Walter J. Hill of the Seattle Zoo supplied a silver pheasant and peafowl. At Cornell University Dr. Charles G. Sibley preserved a specimen of red jungle fowl donated by Dr. J. H. Bruckner; Dr. F. B. Hutt supplied information concerning the source of the Cornell jungle fowl colony. Dr. Herbert M. Hale, Director of the South Australian Museum, donated a specimen of the Mallee fowl (*Leipoa ocellata*); William F. Palsson of Halldorsstadir, Iceland, supplied a rock ptarmigan; Dr. Robert Rausch of Anchorage, Alaska, two willow ptarmigan; Dr. S. Dillon Ripley of Yale University, a trunk of the Megapode *Eulipoa wallacei*; Dr. Ram S. Singh of the British Guiana Museum, two *Opisthocomus hoazin*, one *Crax nigra* and two *Penelope marail*; Dr. M. Alvarez del Toro of Chiapas, Mexico, one *Ortalis vetula*; D. A. Lancaster of Louisiana State University supplied two *Odontophorus guttatus*; James C. Stout of the Washington State Department of Game, two *Callipepla squamata*. Mrs. Phyllis M. Redshaw assisted by preserving specimens and making preliminary dissections.

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## MATERIAL AND METHODS

Specimens were prepared and studied as described by Hudson (1937). Complete dissections were made in those listed below unless indicated otherwise; numbers refer to legs examined, not entire specimens. In addition thirty-nine pairs of turkey feet (*Meleagris*) were used to check certain points.

Family Megapodiidae	
<i>Megapodius pritchardii</i> .....	(juv.) 1
<i>Eulipoa wallacei</i> .....	(above knee) 2
<i>Leipoa ocellata</i> .....	2
Family Cracidae	
<i>Crax nigra</i> .....	2
<i>Penelope marail</i> .....	4
<i>Ortalis vetula</i> .....	2
<i>Ortalis canicollis</i> .....	1
<i>Pipile cumanensis</i> .....	(partial dissection on another) 1
Family Tetraonidae	
<i>Dendragapus obscurus</i> .....	7
<i>Lagopus lagopus</i> .....	4
<i>Lagopus mutus</i> .....	2
<i>Canachites canadensis franklinii</i> .....	4
<i>Bonasa umbellus</i> .....	4
<i>Pedioecetes phasianellus</i> .....	(4 juv.) 8
<i>Tympanuchus cupido</i> .....	2
<i>Centrocerus urophasianus</i> .....	(2 above heel) 4
Family Phasianidae	
<i>Oreortyx picta</i> .....	4
<i>Lophortyx californica</i> .....	6
<i>Callipepla squamata</i> .....	(partial dissection) 4
<i>Colinus virginianus</i> .....	9
<i>Odontophorus guttatus</i> .....	(partial dissection) 4
<i>Alectoris graeca</i> .....	4
<i>Perdix perdix</i> .....	6
<i>Gennaeus nycthemerus</i> .....	2
<i>Gallus gallus</i> (domestic) .....	8
<i>Gallus gallus</i> (red jungle fowl) .....	2
<i>Phasianus colchicus</i> .....	4
<i>Pavo cristatus</i> .....	2
Family Numididae	
<i>Numida meleagris</i> (domestic) .....	5
Family Meleagrididae	
<i>Meleagris gallopavo</i> .....	(2 juv.) 4
Family Opisthocomidae	
<i>Opisthocomus hoazin</i> .....	(1 juv.) 5

In determining the length of bellies or tendons, we measured from the proximal end of the major bone concerned, either the femur, tibiotarsus, or tarsometatarsus. In cases where the structure of a muscle or tendon is expressed as a fraction of such a bone, for example,

.36 femur, it may be assumed that this means the proximal 36 percent of this bone.

#### REVIEW OF THE MUSCLES OF THE PELVIC LIMB

##### *M. iliotrochantericus posterior* (Il. troc. post.)

*Description for Dendragapus* (Figs 2, 3, 6).—This is the largest of the iliotrochanteric muscles. It occupies most of the lateral surface of the preacetabular ilium. The belly narrows slightly posteriorly and, just before inserting on the lateral surface of the trochanter, forms a strong, flat tendon. The Il. troc. post. is covered anteriorly by the sartorius, and dorsally by the aponeurosis of the Il. tib.

*Comparison.*—Similar in all forms examined, but varies with the shape of the preacetabular ilium.

##### *M. iliotrochantericus anterior* (Il. troc. ant.)

*Description for Dendragapus* (Figs. 2-7, 14).—The origin is partly fleshy from a long narrow line along the ventrolateral side of most of the anterior half of the preacetabular ilium, anterior and ventral to the lateral edge of the Il. troc. post. The belly narrows to form a flat tendon which inserts on the anterolateral surface of the femur, slightly distal and anterior to the insertion of the Isch. fem. Laterally the tendon is partly covered by the proximal end of the lateral portion of the belly of the Fem. tib. med.

*Comparison.*—Very uniform except that the insertion is partly fleshy in *Leipoa*, *Eulipoa*, and *Gallus*; tendinous in all others.

In two legs of *Lagopus mutus* the tendon of insertion of the Il. troc. ant. is relatively much narrower than in four legs of *Lagopus lagopus*. The ratio of width of tendon compared to total length of muscle in *L. mutus* is about six percent; in *L. lagopus*, about ten percent.

##### *M. iliotrochantericus medius* (Il. troc. med.)

*Description for Dendragapus* (Figs. 2-7).—This is quite distinct from the other iliotrochanteric muscles and is by far the smallest of the three. It arises fleshy from the ventrolateral surface of the ilium just in front of the acetabulum. It inserts by a flat independent tendon on the lateral side of the femur between the insertions of the Il. troc. ant. and Il. troc. post.

*Comparison.*—The Il. troc. med. is a distinct and separate muscle in all specimens examined with the exception of *Opisthocomus*. In all six legs of *Opisthocomus* the Il. troc. med. is not present as a separate muscle, but is completely fused throughout with the Il. troc. ant.

In one specimen of the silky fowl there is a supernumerary muscle slip located between the bellies of the sartorius and Il. troc. ant. and post. It seems to begin near the origin of the ambiens and passes anteriolaterally over the lateral surface of the Il. troc. ant. and Il. troc. post., becoming tendinous as it approaches the origin of the sartorius. This slip is well developed on the right side, and is present, but much weaker, on the left side.

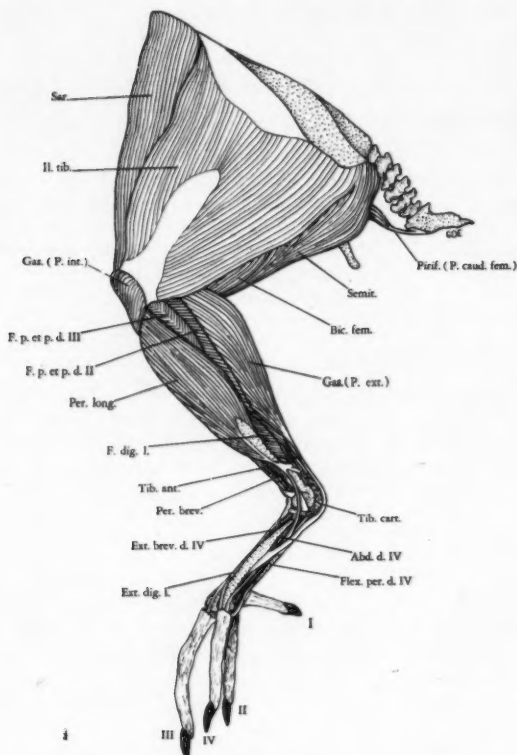


Fig. 1.—Blue grouse (*Dendragapus obscurus*). Lateral view of the superficial muscles of the left leg.

*M. glutaeus medius et minimus* (Glut. med. et min.)

*Description for Dendragapus* (Figs. 3, 4).—This small, flat, triangular muscle has a fleshy origin from the lateral ridge of the ilium, posterior and dorsal to the acetabulum. The flat tendon formed at the proximal limit of the femur inserts on the lateral surface of the distal edge of the trochanter adjacent to the anterior edge of the insertion of the Isch. fem. Laterally the muscle is covered by the Il. tib. and Bic. fem.

*Comparison*.—The Glut. med. et min. shows the weakest development in *Centrocerus*, especially in a specimen from Washington, in which no trace of the muscle can be found on the left side. The variations in relative size are noted below.

Origin more extensive, including all of acetabular ilium: *Megapodius*,

*Eulipoa*, *Leipoa*, *Crax*, *Penelope*, *Gallus* (Cornish fowl, jungle fowl) and *Numida*.

Origin intermediate: *Ortalis*, *Pipile*, *Bonasa*, *Tympanuchus*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Perdix*, *Gennaeus*, *Gallus* (leghorn and silky fowl), *Phasianus*, *Pavo* and *Opisthocomus*.

Origin weak and more posteriorly situated: *Dendragapus*, *Lagopus*, *Canachites*, *Pedioecetes*, *Centrocercus* and *Meleagris*.

In the specimen of *Crax nigra* the tendon terminates about opposite the anteroproximal edge of the Isch. fem., whereas, in other forms the tendon extends to the distal edge.

#### *M. iliacus* (Iliacus)

*Description for Dendragapus* (Figs. 6, 7).—This small, entirely fleshy muscle originates from the ventral border of the ilium just medial to the origin of the Il. troc. med. It passes diagonally posterodistally to insert on the posteromedial side of the shaft of the femur proximal to the Fem. tib. int.

*Comparison*.—Very similar in all forms examined but unusually stout in *Gallus*.

#### *M. ambiens* (Ambiens)

*Description for Dendragapus* (Figs. 3, 4, 6, 7, 14, 15).—This narrow, spindle-shaped muscle arises tendinous or partly fleshy from the pectineal process of the ilium. The belly narrows distally to the tendon which passes between the Fem. tib. med. and sartorius, and extends around the knee within the patellar tendon to the lateral side, thence along the anterior surface of the *Caput fibulae* to join the tendinous origin of the lateral heads of the flexor perforatus muscles. The ambiens tendon is not attached directly to the bellies of the flexor perforatus muscles but inserts upon the tendinous head of origin of these muscles arising from the *Caput fibulae*. In eight specimens the point on the femur opposite the distal end of the belly ranged from 51 percent to 72 percent of the total length of the femur as measured from the proximal end.

*Comparison*.—Variation in attachment of the origin and in belly width is as follows:

Origin not by a distinct tendon: *Megapodius*, *Eulipoa*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus* (2 legs), *Canachites* (3 legs), *Bonasa* (1 leg), *Pedioecetes* (1 leg), *Centrocercus* (3 legs), *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Perdix*, *Gennaeus*, *Gallus*, *Phasianus*, *Pavo*, *Numida* and *Meleagris*.

Origin by a distinct tendon: *Dendragapus* (6 legs), *Lagopus*, *Canachites* (1 leg), *Bonasa* (3 legs), *Pedioecetes* (5 legs), *Tympanuchus*, *Centrocercus* (1 leg) and *Opisthocomus*.

Belly broad: *Megapodius* and *Eulipoa*.

Belly intermediate: *Penelope*, *Ortalis*, *Colinus*, *Gennaeus*, *Gallus*, *Phasianus*, *Pavo*, *Numida* and *Meleagris*.

Belly narrow: *Leipoa*, *Crax*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Lophortyx*, *Alectoris*, *Pedix* and *Opisthocomus*.

The shortest bellies were noted in *Penelope*, *Centrocercus*, *Oreortyx* and *Opisthocomus*, ending about midway the femur or a little below; longest in *Megapodius*, *Leipoa* and *Pavo*, ending about .8 femur or below. Other forms are intermediate.

In two adults of *Opisthocomus* the tendon of origin of the ambiens is short, but in a juvenile specimen the origin is by a long thread-like tendon. The insertion in *Opisthocomus* differs from all other forms examined in that the tendon disappears in the knee region without ever reaching the tendinous origin of the lateral heads of the flexor perforatus muscles.

*M. sartorius* (Sar.)

*Description for Dendragapus* (Figs. 1, 6, 7, 14, 15).—This fleshy band makes up the anterior limit of the thigh. The origin is aponeurotic from the anterodorsal edge of the ilium. There is a strong tendinous connection with the anteroventral edge of the ilium and the belly of the Il. troc. post. Insertion is tendinous on the tibial crest and adjacent patellar tendon, in common with the Il. tib. and Fem. tib. The posterior edge of the muscle is largely fused with the Il. tib.

*Comparison*.—No differences were noted other than minor variations in relative width, the belly being broadest in *Leipoa*, *Pedioecetes*, *Colinus*, *Perdix*, *Gennaeus*, *Phasianus* and *Numida*.

*M. iliotibialis* (Il. tib.)

*Description for Dendragapus* (Figs. 1, 14, 15).—This large triangular muscle comprises most of the lateral surface of the thigh. The origin from a narrow line along most of the dorsolateral ridge of the ilium is aponeurotic anteriorly and fleshy posteriorly. There is also a tendinous connection with the posterior part of the ischium caudal to the belly of the Isch. fem. The Il. tib. is closely attached to the sartorius anteriorly and to the semitendinosus posteriorly. In the distal half of the thigh the middle portion of the belly is aponeurotic and is fused to the underlying Fem. tib. At the knee the Il. tib. joins the Fem. tib. and sartorius to form the patellar tendon which inserts on the anterior tibial crest.

*Comparison*.—The Il. tib. is very uniformly developed in the various forms examined. However in *Opisthocomus* the posterior portion of the origin is mostly or entirely tendinous; it is at least partly fleshy in all others. *Gallus*, *Numida* and *Meleagris* are peculiar in that the posterior edge of the origin has a mostly fleshy, instead of tendinous, attachment to the posterior portion of the ischium.

*M. femoritibialis* (Fem. tib.)

*Description for Dendragapus*:

*M. femoritibialis externus* (Fem. tib. ext.).—This is the smallest of the three femoritibialis muscles (Figs. 3, 15). It arises mostly fleshy from the lateral surface of a little less than the distal half of the shaft of the femur and inserts on the patellar tendon in common with the Fem. tib. med. and Il. tib. Posteriorly the belly of this mus-



cle is closely attached to the overlying Fem. tib. med. and the separation between the two is easily overlooked as was done by Hudson (1937) in *Pedioecetes* and *Colinus*.

*M. femoritibialis medius* (Fem. tib. med.)—This is the largest of the three heads of the Fem. tib. and makes up the bulk of the anterolateral thigh musculature (Figs. 2, 6, 7, 14, 15). It arises fleshy from a very extensive area on the lateral and anterior surfaces of the femoral shaft from the trochanter to the distal condyles. At the proximal end the belly is notched to accommodate the tendon of in-

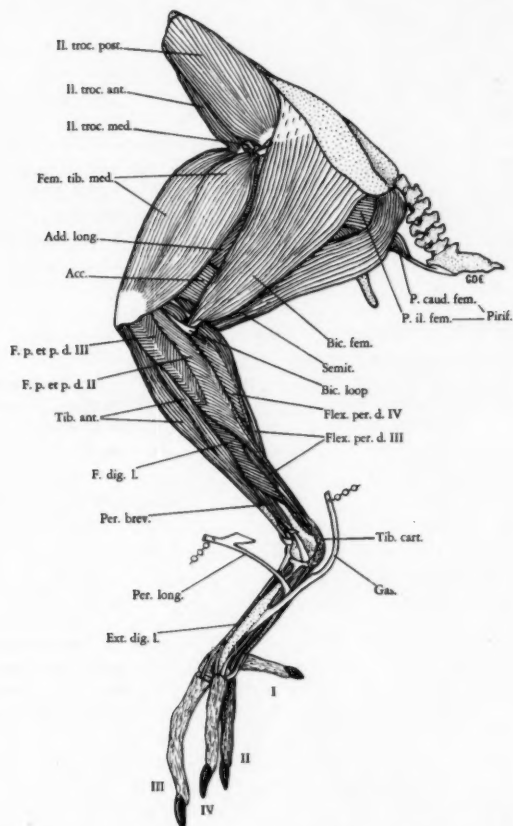


Fig. 2.—Blue grouse (*Dendragapus obscurus*). Lateral view of left leg showing a second layer of muscles. The following have been wholly or partly removed: Sar., Il. tib., Gas., Per. long.

section of the Il. troc. ant. The insertion contributes to the formation of the patellar tendon.

*M. femorotibialis internus* (Fem. tib. int.).—This long narrow belly arises fleshy from the medial surface of almost the entire length of the shaft of the femur (Figs. 6, 7, 15). Distally it forms a strong flat tendon which inserts on the anterior tibial crest in common with the patellar tendon. Near the distal end there is an indication of a division into a deep and a superficial layer.

*Comparison*.—The Fem. tib. ext. is longest in *Megapodius*, *Eulipoa* and *Leipoa*, extending almost up to the Isch. fem. insertion; not quite so long in *Crax*. It is shortest in *Lagopus*, *Centrocercus* and

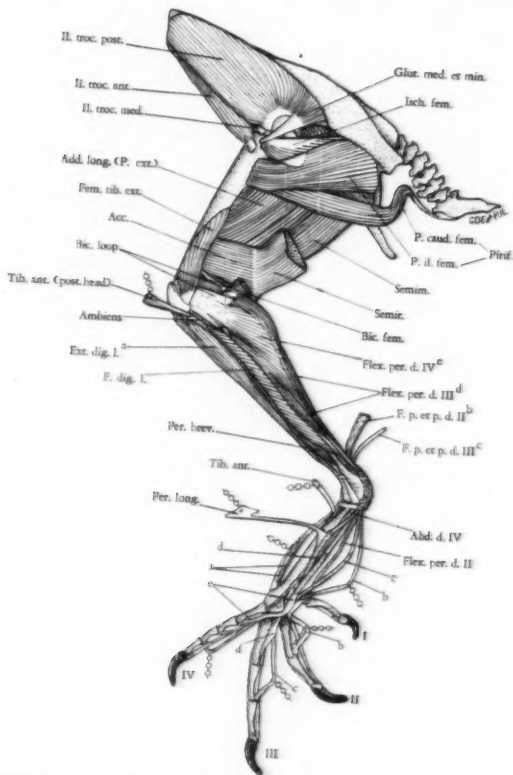


Fig. 3.—Blue grouse (*Dendragapus obscurus*). Lateral view of left leg showing a third layer of muscles. In addition to those listed for Fig. 2, the following have been wholly or partly removed: Fem. tib. med., Bic. fem., Semit., Tib. ant., F. p. et p. d. II, and F. p. et p. d. III.

*Opisthocomus*, confined to less than the distal half of the femur; intermediate in other forms.

The Fem. tib. med. is typical in all forms examined. The division of the Fem. tib. int. into a superficial and deep layer is more or less clearly indicated in all forms examined with the possible exception of *Megapodius* and *Eulipoa*; generally there is a superficial tendinous sheet on the medial side near the distal end, but this is fleshy in *Gallus* and *Pavo*.

#### *M. piriformis* (Pirif.)

*Description for Dendragapus*.—This muscle is composed of the *Pars caudifemoralis* and the *Pars iliofemoralis* which are separate for most of their extent but have a common insertion (Figs. 3, 4).

The *Pars caudifemoralis* (P. caud. fem.) arises by a narrow tendon from a heavy tendinous sheet on the ventrolateral surface of the pygostyle. The flat, spindle-shaped belly passes medial to the semitendinosus and Bic. fem. to join the P. il. fem. (Figs. 1, 2, 6, 7, 14).

The dorsal portion of the origin of the *Pars iliofemoralis* (P. il. fem.) arises fleshy from a narrow line along the ventral edge of the lateral ridge of the ilium, continuous with the ventral portion which arises fleshy from a narrow line on the posterolateral surface of the ischium. This muscle is covered laterally by the Bic. fem. and the Il. tib. (Fig. 14). The belly of the P. il. fem. is about twice the width of the P. caud. fem. and encloses a triangular tendinous area along the dorsal edge opposite the point of fusion with the P. caud. fem. The common insertion of the Pirif., on the posterior surface of the femur distal to the insertion of the Isch. fem., is almost entirely fleshy, but the mediodistal edge, representing a continuation of the P. caud. fem., sends a few tendinous fibers to the femur.

*Comparison*.—Both parts are present in all except *Meleagris* in which the P. caud. fem. is absent. In *Pavo* the P. caud. fem. is very weak and has no connection with the pygostyle but arises from the fascia just posterior to the ischium. The following variations were noted in regard to the origin of the P. caud. fem. in other forms.

No distinct tendon of origin: *Leipoa*, *Penelope*, *Ortalis*, *Pipile*, *Colinus* (2 legs), *Alectoris*, *Gallus* (jungle fowl), *Gennaeus* (1 leg), *Phasianus* (1 leg) and *Opisthocomus*.

Origin by a short tendon: *Megapodius*, *Crax*, *Oreortyx*, *Lophortyx*, *Colinus* (2 legs), *Perdix*, *Gennaeus* (1 leg), *Gallus* (Cornish fowl), *Phasianus* (2 legs) and *Numida*.

Origin by a longer tendon: *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus* and *Gallus* (leghorn, silky fowl).

In *Crax*, *Pedioecetes*, *Tympanuchus*, *Gennaeus*, and the silky fowl the belly of the P. caud. fem. is narrow, being distinctly less than half the width of the P. il. fem.; narrowest in *Pavo*, about one-ninth the width of P. il. fem. The belly is unusually wide in *Oreortyx*, *Colinus*, and especially *Alectoris*, and shows the greatest relative width in *Opisthocomus*. In other forms the belly of the P. caud. fem. is about half the width of the P. il. fem. In *Crax* the P. caud. fem. fuses with

sertion of the II. troc. ant. The insertion contributes to the formation of the patellar tendon.

*M. femoritibialis internus* (Fem. tib. int.).—This long narrow belly arises fleshy from the medial surface of almost the entire length of the shaft of the femur (Figs. 6, 7, 15). Distally it forms a strong flat tendon which inserts on the anterior tibial crest in common with the patellar tendon. Near the distal end there is an indication of a division into a deep and a superficial layer.

*Comparison.*—The Fem. tib. ext. is longest in *Megapodius*, *Eulipoa* and *Leipoa*, extending almost up to the Isch. fem. insertion; not quite so long in *Crax*. It is shortest in *Lagopus*, *Centrocercus* and

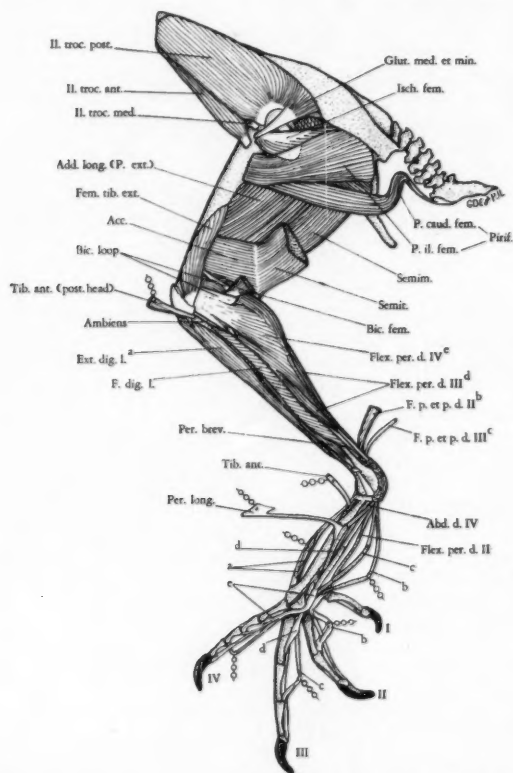


Fig. 3.—Blue grouse (*Dendragapus obscurus*). Lateral view of left leg showing a third layer of muscles. In addition to those listed for Fig. 2, the following have been wholly or partly removed: Fem. tib. med., Bic. fem., Semit., Tib. ant., F. p. et p. d. II, and F. p. et p. d. III.

*Opisthocomus*, confined to less than the distal half of the femur; intermediate in other forms.

The Fem. tib. med. is typical in all forms examined. The division of the Fem. tib. int. into a superficial and deep layer is more or less clearly indicated in all forms examined with the possible exception of *Megapodius* and *Eulipoa*; generally there is a superficial tendinous sheet on the medial side near the distal end, but this is fleshy in *Gallus* and *Pavo*.

*M. piriformis* (Pirif.)

*Description for Dendragapus*.—This muscle is composed of the *Pars caudifemoralis* and the *Pars iliofemoralis* which are separate for most of their extent but have a common insertion (Figs. 3, 4).

The *Pars caudifemoralis* (P. caud. fem.) arises by a narrow tendon from a heavy tendinous sheet on the ventrolateral surface of the pygostyle. The flat, spindle-shaped belly passes medial to the semitendinosus and Bic. fem. to join the P. il. fem. (Figs. 1, 2, 6, 7, 14).

The dorsal portion of the origin of the *Pars iliofemoralis* (P. il. fem.) arises fleshy from a narrow line along the ventral edge of the lateral ridge of the ilium, continuous with the ventral portion which arises fleshy from a narrow line on the posterolateral surface of the ischium. This muscle is covered laterally by the Bic. fem. and the Il. tib. (Fig. 14). The belly of the P. il. fem. is about twice the width of the P. caud. fem. and encloses a triangular tendinous area along the dorsal edge opposite the point of fusion with the P. caud. fem. The common insertion of the Pirif., on the posterior surface of the femur distal to the insertion of the Isch. fem., is almost entirely fleshy, but the mediolateral edge, representing a continuation of the P. caud. fem., sends a few tendinous fibers to the femur.

*Comparison*.—Both parts are present in all except *Meleagris* in which the P. caud. fem. is absent. In *Pavo* the P. caud. fem. is very weak and has no connection with the pygostyle but arises from the fascia just posterior to the ischium. The following variations were noted in regard to the origin of the P. caud. fem. in other forms.

No distinct tendon of origin: *Leipoa*, *Penelope*, *Ortalis*, *Pipile*, *Colinus* (2 legs), *Alectoris*, *Gallus* (jungle fowl), *Gennaeus* (1 leg), *Phasianus* (1 leg) and *Opisthocomus*.

Origin by a short tendon: *Megapodius*, *Crax*, *Oreortyx*, *Lophortyx*, *Colinus* (2 legs), *Perdix*, *Gennaeus* (1 leg), *Gallus* (Cornish fowl), *Phasianus* (2 legs) and *Numida*.

Origin by a longer tendon: *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus* and *Gallus* (leghorn, silky fowl).

In *Crax*, *Pedioecetes*, *Tympanuchus*, *Gennaeus*, and the silky fowl the belly of the P. caud. fem. is narrow, being distinctly less than half the width of the P. il. fem.; narrowest in *Pavo*, about one-ninth the width of P. il. fem. The belly is unusually wide in *Oreortyx*, *Colinus*, and especially *Alectoris*, and shows the greatest relative width in *Opisthocomus*. In other forms the belly of the P. caud. fem. is about half the width of the P. il. fem. In *Crax* the P. caud. fem. fuses with

the P. il. fem. at least one inch posterior to the femur; the fusion is much closer to the femur in other forms.

The tendinous area on the dorsal side of the P. il. fem. is present in all except *Opisthocomus*.

*M. semitendinosus* (Semit.)

*Description for Dendragapus* (Figs. 1-4, 6, 7, 14, 15).—This is the fleshy band forming the posterior limit of the thigh musculature. The origin is fleshy from the posterior edge of the ilium and partly fleshy from the transverse processes of about the two anterior free caudal vertebrae. The proximal part of the belly is strongly attached to the posterior edge of the Il. tib. The belly extends distally to form a tendinous insertion in common with the semimembranosus. This tendon passes between the middle and inner heads of the gastrocnemius before inserting on the medial surface of the tibia, just distal to the *Caput tibiae*. The anterior edge of the distal end of the belly of the semitendinosus is connected by a fibrous raphe to the Accessory semitendinosus muscle (Acc.), which has an extensive fleshy attachment on the posterolateral surface of the distal part of the shaft of the femur.

*Comparison*.—The connection with the proximal caudal vertebrae is present in all forms except *Opisthocomus*, in which the origin is entirely from the posterolateral surface of the ilium. In *Ortalis* the origin shows the usual connection with the proximal caudal vertebrae and ilium, but also extends downward onto the ischium. The semitendinosus is well developed in all forms examined but reaches its maximum relative width in *Pedioecetes*.

The insertion of the accessorius is most extensive in *Pedioecetes*, reaching far above the middle of the femoral shaft; extends up to middle of femoral shaft or a little above in *Crax*, *Ortalis*, *Numida* and *Opisthocomus*. In all others the insertion is usually confined to much less than the distal half of the femoral shaft.

*M. semimembranosus* (Semim.)

*Description for Dendragapus* (Figs. 3, 4, 6, 7, 14, 15).—This muscle makes up the posterior border of the thigh musculature on the medial side. It arises mostly tendinous from a narrow line on the posterolateral edge of the ischium and adjacent pubis, ventral to the posterior portion of the Isch. fem. Posterior to the knee the semimembranosus becomes tendinous before joining with the semitendinosus to contribute to their common insertion. This combined tendon is intimately attached to the medial surface of the P. med. M. gas.

*Comparison*.—The Semim. shows the maximum strength and width in *Megapodius*, *Eulipoa*, *Leipoa*, *Tympanuchus*, and *Pedioecetes*; it is weakest in *Dendragapus*, *Bonasa*, *Centrocercus* and *Numida*, and intermediate in all others.

In *Crax*, *Penelope*, *Ortalis*, *Pipile* and *Numida* the semimembranosus is situated more anteriorly than in other forms, the center of the origin being about midway between the posterior edge of the



ischium and the femur. The middle of the origin is a little behind this in *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Gennaeus*, *Pavo* and *Meleagris*; a little farther posterior in *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix* and *Phasianus*. The center of origin is most posteriorly situated in *Leipoa* and *Opisthocomus*. In *Phasianus* the belly is distinctly wider in the male than in the female. In *Opisthocomus* the origin is unusually high on the pelvis, arising almost entirely fleshy from the ischium without any connection with the pubis.

*M. biceps femoris* (Bic. fem.)

*Description for Dendragapus* (Figs. 1-4, 10, 14, 15).—The origin is from a long narrow line along the dorsolateral ridge of the ilium just ventral to the origin of the Il. tib. The anterior edge of the origin is tendinous and the remainder fleshy. Proximally the belly is strongly attached to the overlying Il. tib. Posterior to the knee the converging fibers form a round tendon which passes through the biceps loop and continues distally to insert on a slight tubercle on the posterolateral surface of the fibula.

*Comparison*.—No important variations were noted.

*M. ischiofemoralis* (Isch. fem.)

*Description for Dendragapus* (Figs. 3, 4).—Arises fleshy from most of the lateral surface of the ischium and from the outer surface of the tendinous sheet occupying the posterior portion of the ilio-ischiadic foramen. Anteriorly the fibers converge to form a flat tendon which inserts on the lateral surface of the trochanter immediately posterior to the insertion of the Glut. med. et min. and proximal to the origin of the Fem. tib. med. Laterally the belly is covered mainly by the P. il. fem. of the Pirif.

*Comparison*.—The Isch. fem. is shortest in *Ortalis*, *Penelope*, *Crax*, *Tympanuchus*, *Pedioecetes*, and *Meleagris*, the origin being limited to about the anterior two-thirds to three-fourths of the ischium; similar to *Dendragapus* in other forms examined.

*M. obturator internus* (Obt. int.)

*Description for Dendragapus* (Figs. 4-7).—This large triangular muscle arises fleshy from an extensive area on the medial surface of the postacetabular pelvis, including part of the pubis, most of the ischium and a small area on the ventrolateral surface of the ilium. Anteriorly the muscle enters the obturator foramen and passes to the outside of the pelvis, forming a strong tendon which inserts on the posterolateral side of the trochanter of the femur, posterior to the insertion of the Il. troc. post. Some of the fleshy fibers that accompany the tendon almost to the insertion arise from the dorsal and anterior margins of the lateral surface of the obturator foramen.

*Comparison*.—The dorsal edge of the Obt. int., arising from the

ventrolateral surface of the ilium, shows great variation in extent, as indicated below.

Very weak: *Lagopus*, *Canachites*, *Pedioecetes* and *Tympanuchus*.

Small: *Dendragapus*, *Bonasa*, *Centrocercus* and *Meleagris*.

Large: *Megapodius*, *Eulipoa*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Perdix*, *Gallus*, *Gennaeus*, *Phasianus*, *Pavo* and *Numida*.

In *Opisthocomus* there is no connection whatever with the ventrolateral surface of the ilium.

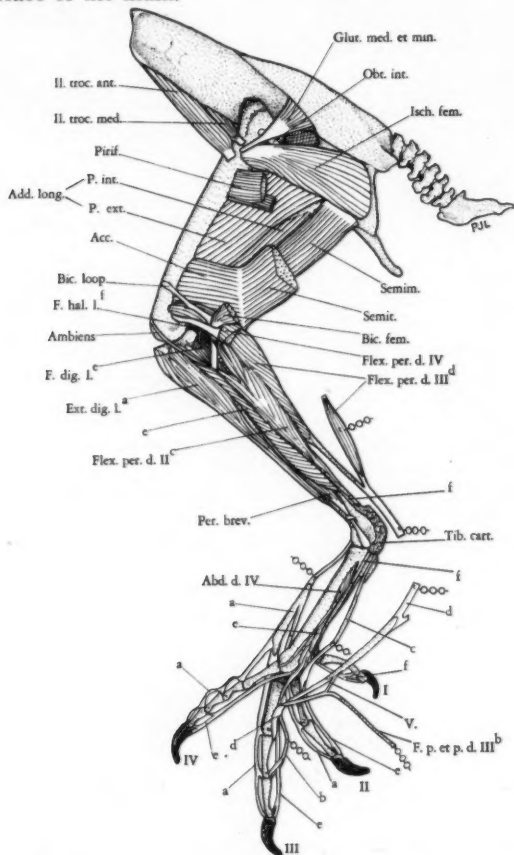


Fig. 4.—Blue grouse (*Dendragapus obscurus*). Lateral view of left leg showing a fourth layer of muscles. In addition to those listed for Fig. 3 the following have been wholly or partly removed: Il. troc. post., Pirif., Fem. tib. ext., Flex. per. d. III and Flex. per. d. IV.



*Comparison.*—Very similar in all forms studied except *Gennaeus*, *Pavo* and *Meleagris* in which the muscle appears to be divided into two slips which insert separately on the femur.

*M. adductor longus et brevis* (Add. long.)

*Description for Dendragapus* (Figs. 2-7, 14, 15).—This muscle is divided into two distinct heads. The P. ext. arises mainly fleshy from a long line on the ventral edge of a little more than the anterior half of the ischium and to a slight extent from the adjacent pubis. The origin of the P. int. is directly ventral and adjacent to that of the P. ext. but extends slightly farther anteriorly and posteriorly. Anteriorly the origin of the P. int. is fleshy and posteriorly it is tendinous.

The two heads have adjacent insertions on the posterior border of the shaft of the femur beginning just below the insertion of the Pirif. and extending to the condyles. The P. int. is somewhat larger than the P. ext. and has a more extensive insertion on the femur.

*Comparison.*—The P. int. is several times as large as the P. ext. in *Tympanuchus* and *Pedioecetes*. It is much stronger than the P. ext. in *Crax*, *Pipile*, *Gennaeus*, *Pavo* and *Meleagris*. They are about equal in size in *Bonasa*; all other forms are intermediate. The P. ext. is short in *Pedioecetes*, the origin anteriorly situated and the insertion not extending more than half way down the femur; similar but a little longer in *Tympanuchus*.

The posteroproximal tendinous sheet in the belly of the P. int. is most extensive in *Megapodius*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris* and *Gennaeus*; smaller in the other forms examined.

Variations in the insertion of the P. int. of the Add. long. were noted as follows:

Mainly by a thin tendinous sheet: *Megapodius*, *Eulipoa*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Oreortyx*, *Lophortyx*, *Colinus*, *Perdix*, *Gallus* (leg-horn), *Phasianus*, *Numida* and *Meleagris*.

Intermediate: *Alectoris*, *Gennaeus*, *Gallus* (Cornish fowl) and *Pavo*.

Fleshy: *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Gallus* (silky fowl, jungle fowl), and *Opisthocomus*.

*M. tibialis anterior* (Tib. ant.)

*Description for Dendragapus* (Figs. 1-3, 6-8, 16-18).—This two-headed muscle is located in the anterior portion of the shank, immediately beneath the Per. long. The larger, anterior head arises partly fleshy from the anterior tibial crest and fleshy from the deep surface of the belly of the Per. long. The much smaller posterior head arises by a short tendon from the distal end of the external condyle of the femur, the tendon passing between the head of the fibula and the lateral tibial crest. The belly fuses with that of the anterior head about midway the shank. Distally the muscle connects with the ossified tendon which becomes flexible before passing beneath the fibrous loop above the distal malleoli. The tendon traverses the intertarsal joint and inserts near the proximal end of the tarsometatarsus on the anteromedial surface (Fig. 8).

*Comparison.*—The following are variations in the length of the belly:

Belly short, ending well above fibrous loop: *Lagopus*, *Canachites*, *Bonasa*, *Tympanuchus*, *Oreortyx*, *Lophortyx*, *Colinus* and *Alectoris*.

Belly intermediate: *Megapodius*, *Crax*, *Dendragapus*, *Pedioecetes*, *Centrocercus*, *Perdix*, *Gennaeus*, *Numida* and *Meleagris*.

Belly long, extending to fibrous loop: *Leipoa*, *Penelope*, *Ortalis*, *Pipile*, *Gallus*, *Phasianus*, *Pavo* and *Opisthocomus*.

The occurrence of a sesamoid in the Tib. ant. in the region of the shank was noted as follows:

Sesamoid present: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.)

Sesamoid absent: *Megapodius* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

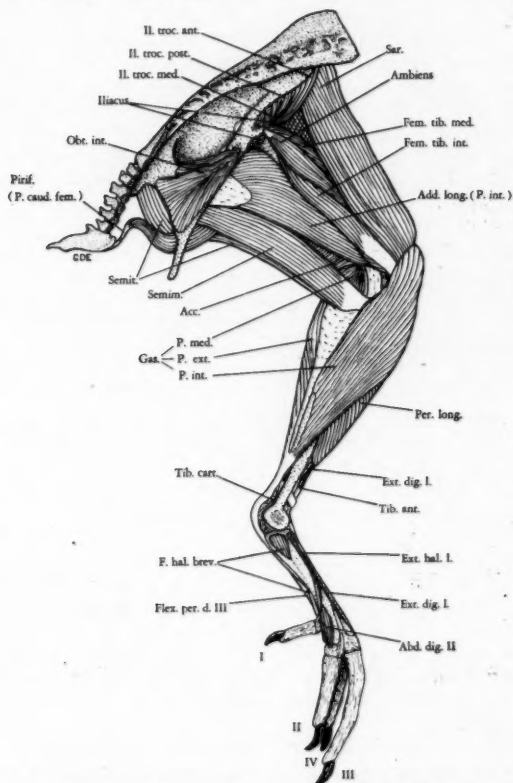


Fig. 6.—Blue grouse (*Dendragapus obscurus*). Medial view of the superficial muscles of the left leg.

An accessory tendon of insertion was noted in a few forms, but its presence or absence, as well as extent, is subject to great individual variation.

*M. extensor digitorum longus* (Ext. dig. 1.)

*Description for Dendragapus* (Figs. 1-4, 6-8, 16-19).—This muscle occupies the anterior surface of the shank immediately posterior to the Tib. ant. The origin is from about the proximal three-fifths of the anterior surface of the tibiotarsus. The belly narrows distally to form a tendon at about the proximal end of the distal fifth of the shank. In the region of the shank the belly and tendon enclose a long sesamoid. After passing through the fibrous loop posterior to the tendon of the Tib. ant. the tendon of the Ext. dig. 1. extends under a bony inter-malleolar loop on the anterior surface of the tibiotarsus; near the proximal end of the tarsometatarsus it passes beneath a fibrous loop on the anteromedial surface. About midway the tarsometatarsus the tendon bifurcates. The smaller medial branch supplies Dig. II and sends a tendon to the medial side of Dig. III; the larger lateral branch bifurcates, sending tendons to the lateral side of Dig. III and to Dig. IV. Along most of the anterior surface of the tarsometatarsus the main tendon of the Ext. dig. 1. is ossified. The tendons supplying the digits are rather vaguely defined, being bound together by tendinous sheets; they are rather diffuse beyond the first phalanx of each digit.

*Second digit.* There are two tendons supplying the second digit. One is short and inserts mainly on the medial edge of the proximal end of the second phalanx. The longer tendon passes down the anterolateral side to insert on the proximal end of the ungual phalanx. In addition to these there is a strong tendinous attachment to the proximal end of the proximal phalanx and the proximal end of the second phalanx.

*Third digit.* There are two tendons to the third digit. The medial one which arises mainly from the tendon supplying the second digit is short and inserts mostly on the proximal end of the second phalanx. The long lateral branch to the third digit has a rather vaguely defined division opposite the second phalanx; the medial of these inserts mainly on the base of the third phalanx and the lateral branch inserts mainly on the ungual phalanx. There is also a strong attachment to the proximal end of the proximal phalanx.

*Fourth digit.* The branch to the fourth digit inserts mainly on the bases of the second, third, fourth and fifth phalanges.

*Comparison.*—The belly of the Ext. dig. 1. is narrow, leaving much of the anterolateral surface of the tibiotarsus exposed in *Crax*, *Penelope*, and *Pipile*; belly broad and heavy in *Opisthocomus*, almost or entirely covering the anterolateral surface of the tibiotarsus; all others intermediate.

In most forms examined the bifurcation of the tendon is about midway the tarsometatarsus; most proximal in *Ortalis*, *Canachites*, *Bonasa*, *Alectoris*, *Perdix*, and *Numida*, being above the middle; well below the middle in *Megapodius*, *Leipoa*, *Lagopus*, and *Pavo*. In



*Opisthocomus* the main tendon of the Ext. dig. I. does not bifurcate, as in other forms studied, but simply gives off, near the distal end of the tarsometatarsus, an undivided branch to each foretoe. Divided tendons along the proximal portions of Digits II and III, as described for *Dendragapus*, are typical of all other forms examined.

Sesamoids in the Ext. dig. I. were noted as follows:

Present in shank and tarsus: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

Present in tarsus only: *Gallus*.

No sesamoids present: *Megapodius* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

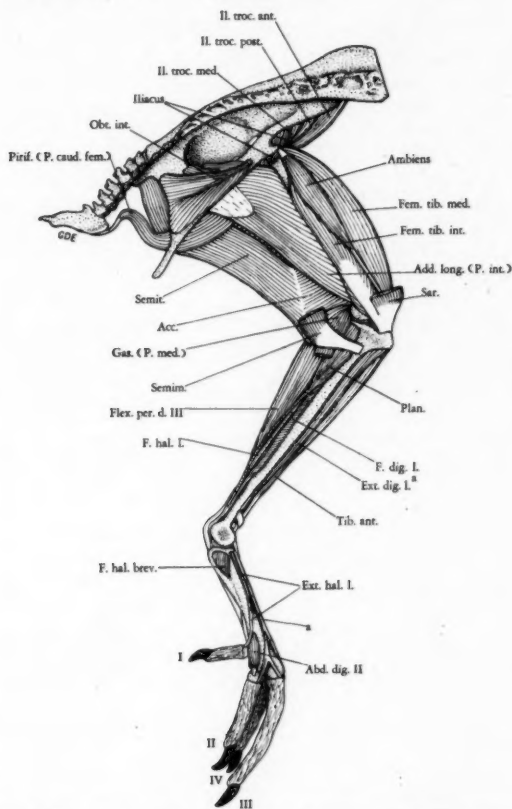


Fig. 7.—Blue grouse (*Dendragapus obscurus*). Medial view of left leg showing a second layer of muscles. The following have been wholly or partly removed: Sar., Semim., Gas.

In *Lophortyx*, *Colinus*, *Alectoris*, *Numida* and *Opisthocomus* no sesamoids were present even though fully adult specimens were studied.

In one leg of *Bonasa* there is a distinct muscular slip from the anterior surface of the tarsometatarsus just distal to the insertion of the Tib. ant. It inserts on the medial branch of the tendon of the Ext. dig. 1., which in this specimen bifurcates above the insertion of the Tib. ant.

In both legs of one specimen of silky fowl the tendon of the Ext. dig. 1. gives off a supernumerary branch on the medial side near the proximal end of the tarsometatarsus. This bifurcates distally sending a branch to each part of the double hallux.

*M. peronaeus longus* (Per. long.)

*Description for Dendragapus* (Figs. 1-3, 6, 8, 9, 16-18). — This large muscle occupies the anterior and anterolateral surface of the shank. It arises from the knee fascia, the anterior tibial crest, from the belly of the underlying Tib. ant., from the anterior edge of the belly of the F. p. et p. d. III, from the lateral edge of the belly of the F. dig. 1, and from a narrow line along the anteromedial surface of the tibiotarsus. The belly narrows distally, forming an ossified tendon at about the beginning of the distal fourth of the shank. Just above the malleoli the tendon is unossified and sends a short posterior branch to the proximal end of the lateral side of the tibial cartilage. The anterior branch continues distally over the lateral side of the intertarsal joint and inserts broadly on the anterior edge of the ossified tendon of the Flex. per. d. III opposite the second fourth of the tarsometatarsus.

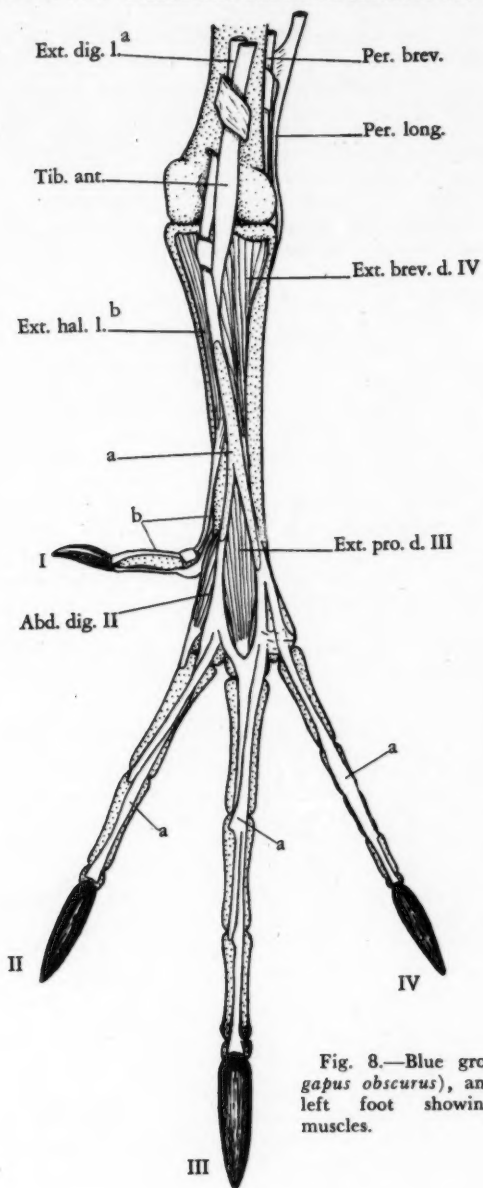
*Comparison.*—In most forms the development of the belly is very similar to *Dendragapus*; in *Oreortyx*, *Lophortyx*, *Colinus*, *Perdix*, and *Alectoris* the belly is shorter, limited to about the proximal two-thirds of the shank; belly long in *Leipoa*, extending almost to the bifurcation.

The Per. long. is very peculiar in *Opisthocomus*: belly short, limited to about the distal two-thirds of the shank, and situated entirely on the lateral side; very narrow above, broad distally. The origin is from the lateral side of the shaft of the fibula and adjacent tibia; also strongly attached to the Per. brev., the F. dig. 1., and adjacent muscles. Near the distal end of the shank the origin extends posteriorly onto the posterolateral surface of the shaft of the tibia. Insertion typical, but the tendon passing to the Flex. per. d. III weak and narrow.

The occurrence of a sesamoid in the region of the shank was noted as follows:

Sesamoid present in shank: *Megapodius*, *Leipoa*, *Crax*, *Ortalis*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

Sesamoid absent in shank: *Penelope*, *Pipile*, *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.



There is a short sesamoid in the main tendon of the Per. long. just above its attachment to the tendon of the Flex. per. d. III in *Phasianus* and most specimens of *Perdix*; this is not present in the other forms. In one specimen of *Perdix* the tendon is strongly attached to the lateral side of the proximal end of the hypotarsus and to the Gas. tendon above the insertion on the tendon of the Flex. per. d. III. Opposite the proximal end of the tarsometatarsus in two specimens of the silky fowl the tendon is strongly attached to the underlying connective tissue in such a way that it appears impossible for the Per. long. to exert any pull on the tendon of the Flex. per. d. III.

*M. peronaeus brevis* (Per. brev.)

*Description for Dendragapus* (Figs. 1-5, 8, 9, 16, 17).—This slender muscle is limited to about the distal three-fifths of the shank. It arises from a narrow line on the lateral surface of the tibiotarsus and from the anterior and medial surfaces of the shaft of the fibula. Near the distal end of the tibia the muscle forms a tendon which passes under a fibrous loop and becomes considerably expanded over the lateral surface of the lateral malleolus. The belly and the proximal end of the tendon enclose a sesamoid. In the intertarsal joint the tendon turns medially to its insertion on the posteroproximal surface of the hypotarsus near the lateral side.

*Comparison*.—The relative length of the entire muscle is very similar in most forms; however in *Bonasa*, *Colinus* and *Opisthocomus* it is somewhat longer.

The following variations were noted in regard to the distal end of the fleshy portion of the belly of the Per. brev. in relation to the fibrous loop.

Belly ends proximal to loop: *Ortalis*, *Lagopus*, *Bonasa*, *Pedioecetes*, *Oreortyx*, *Lophortyx*, *Colinus* and *Perdix* (4 legs).

Intermediate: *Megapodius*, *Leipoa*, *Crax*, *Penelope*, *Pipile*, *Dendragapus*, *Canachites*, *Tympanuchus*, *Centrocercus*, *Alectoris*, *Perdix* (2 legs), *Gennaeus*, *Gallus*, *Phasianus*, *Pavo*, *Numida* and *Meleagris*.

Belly extends below loop: *Opisthocomus*.

In most forms the belly is slender as in *Dendragapus*, but it is relatively stouter in *Leipoa*, *Ortalis*, *Penelope*, *Gallus*, *Numida*, and especially in *Opisthocomus*.

The presence of a sesamoid in the Per. brev. was noted as follows:

Sesamoid present: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

Sesamoid absent: *Megapodius* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

The insertion in *Opisthocomus* is peculiar in that there is a distinct attachment to the posterolateral surface of the head of the tarsometatarsus in addition to the usual attachment to the hypotarsus.

*M. gastrocnemius* (Gas.)

*Description for Dendragapus* (Figs. 1, 2, 6, 16-18).—The Gas. forms the superficial musculature of most of the medial and posterior surfaces of the shank.

*Pars externa* (P. ext.).—Originates by a short tendon from the lateral edge of the external condyle of the femur, between the origin of the medial head of the Flex. per. d. IV and the F. p. et p. d. II. The origin is bound to the proximal end of the underlying lateral arm of the Bic. loop. The belly broadens over the posterolateral surface of the shank and is connected with the P. int. by a thin tendinous sheet.

*Pars media* (P. med.).—This small head arises fleshy from the posterior surface of the internal condyle of the femur, immediately distal to the femoral attachment of the Acc. semit. and the P. int. of the Add. long. The posterior surface of the belly is strongly attached to the Acc. semit. At about the distal end of the proximal third of the shank the P. med. has a tendinous insertion on the P. int.

*Pars interna* (P. int.).—Origin mostly fleshy from the medial surface of the *Caput tibiae*, anterior tibial crest and patellar tendon. At the proximal end the belly extends around the front of the knee for a short distance. The large flat belly covers most of the medial surface of the shank and is attached on its posterior edge to a strong fascia which is closely adherent to the Semit., Semim., and P. med. M. gas. proximally, and the P. ext. M. gas. distally. Both the P. ext. and P. int. contain a sesamoid a short distance proximal to their point of fusion above the tibial cartilage.

The combined tendon covers the posterior surface of the tibial cartilage and forms a tough sheet which holds the flexor tendons in position on the posterior side of the tarsus. The Gas. tendon is extensively attached to the posteromedial and posterolateral surfaces of the tarsometatarsus.

There is a narrow bridge of bone extending from the posterior side of the hypotarsus to the posteromedial edge of the tarsometatarsus, a little above the middle of that bone. This bony bridge apparently represents an ossified portion of the tendon of the Gas.

*Comparison.*—In *Opisthocomus* the belly of the P. int. does not extend around the front of the knee; all other specimens resemble *Dendragapus*.

In some cases the P. int. and P. ext. fuse, forming only a single tendon. In others each part forms a more or less separate tendon, the two uniting farther down the shank.

P. int. and P. ext. with common tendon: *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Gallus* (one old male Cornish fowl, jungle fowl), *Numida* and *Opisthocomus*. Intermediate: *Leipoa* and *Gallus* (leghorn, silky fowl).

P. int. and P. ext. with more or less separate tendons above point of fusion: *Megapodius*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Perdix*, *Genaenus*, *Phasianus*, *Pavo* and *Meleagris*.





The occurrence of sesamoids in the tendons of the P. ext. and P. int. was noted as follows.

Sesamoids present: *Ortalis vetula* (P. ext. only), *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

Sesamoids absent: *Megapodius* (juv.), *Leipoa*, *Crax*, *Penelope*, *Ortalis canicollis*, *Pipile*, *Oreortyx* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

The bony bridge, apparently formed by a part of the tendon of the Gas., varied as follows.

Bony bridge present: *Dendragapus*, *Canachites*, *Lagopus*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Alectoris* (1 leg), *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

Not ossified: *Megapodius* (juv.), *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Centrocercus*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris* (3 legs), *Gallus*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

In *Gennaeus*, *Perdix*, *Pavo*, *Phasianus*, *Tympanuchus* and *Meleagris* the bony bridge extends much farther distally than in other forms, reaching well below the middle of the tarsus.

#### *M. plantaris* (Plan.)

*Description for Dendragapus* (Figs. 5, 7, 9, 10, 16, 17).—This muscle arises fleshy from about the proximal fifth of the posteromedial surface of the tibia. About two-fifths to halfway down the shank the belly forms a slender ossified tendon which passes distally along the posterolateral edge of the P. int. M. gas. to which it is closely attached. Insertion is on the proximal end of the medial side of the tibial cartilage. From the medial side the Plan. is exposed upon removal of the P. int. M. gas.

*Comparison.*—In most forms the belly terminates about two-fifths the way down the tibiotarsus; however, in the following the belly ends about midway: *Leipoa*, a few *Dendragapus*, *Tympanuchus*, some *Pedioecetes*, *Gallus*, and *Opisthocomus*.

Ossification of the tendon was noted as follows:

Sesamoid present: *Leipoa*, *Ortalis*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Gallus* (Cornish fowl, 1 leg), *Phasianus*, *Pavo* and *Meleagris*.

Sesamoid absent: *Megapodius* (juv.), *Crax*, *Penelope*, *Pipile*, *Lophortyx*, *Colinus*, *Alectoris*, *Gallus* (9 legs), *Numida* and *Opisthocomus*.

#### *Position of Flexor Tendons Passing the Intertarsal Joint*

*Description for Dendragapus.*—Removal of the Gas. exposes on the posterolateral side of the tibial cartilage a bundle of three tendons: the broad anteriorly-situated tendon of the Flex. per. d. III which forms a sheath around the Flex. per. d. IV on the lateral side and the F. p. et p. d. III on the medial side.

There are four canals traversing the tibial cartilage. The most superficial, on the posteromedial side, encloses the tendon of the F. p. et p. d. II. The more deeply situated canals enclose the following

tendons: the F. hal. 1. laterally, the Flex. per. d. II near the middle and the F. dig. 1. medially.

In the hypotarsus (Fig. 18) the tendon of the F. hal. 1 runs in a groove on the lateral side; this is not roofed over with bone. The F. p. et p. d. II lies posteromedial to the Flex. per. d. II in a common deep bony groove on the middle of the posterior side of the hypotarsus; this groove may be partly roofed over with a thin sheet of bone. The most deeply situated tendon is that of the F. dig. 1. which runs in a bony canal near the middle of the hypotarsus.

*Comparison.*—No differences were noted in the position of flexor tendons traversing the intertarsal joint. The following variation was found in regard to the tendons of the Flex. per. d. II and F. p. et p. d. II in the hypotarsus.

Both in same fibrous canal: *Pipile*, *Penelope* (3 legs), *Lagopus*, *Bonasa*, *Pedioecetes* (3 legs), *Centrocercus*, *Oreortyx*, *Perdix* (3 legs) and *Gallus* (Cornish fowl, silky fowl, jungle fowl).

Uncertain: *Megapodius*, *Leipoa*, *Ortalis canicollis*, *Dendragapus*, *Lophortyx*, *Colinus*, *Alectoris*, *Gallus* (leghorn) and *Numida*.

Each in a separate fibrous canal: *Crax*, *Penelope* (1 leg), *Ortalis vetula*, *Canachites*, *Pedioecetes* (3 legs), *Tympanuchus*, *Gennaeus*, *Phasianus*, *Pavo*, *Meleagris* and *Opisthocomus*.

The occurrence of a bony roof over the groove in the hypotarsus enclosing the tendons of the Flex. per. d. II and F. p. et p. d. II varied as follows:

Well ossified: *Lophortyx* (2 legs), *Colinus* and *Perdix* (3 legs).

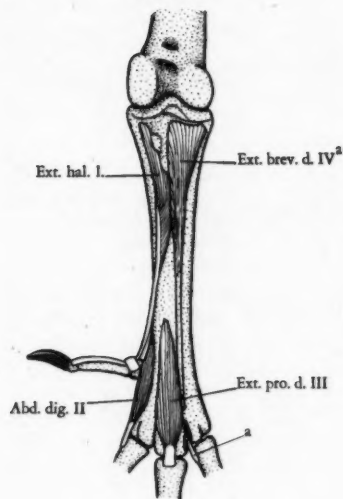
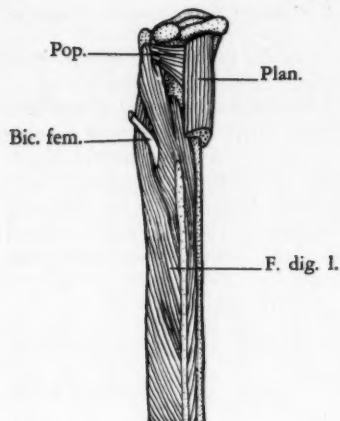
Thinly ossified: *Dendragapus* (a few), *Canachites* and *Pedioecetes* (2 legs).

Not ossified: *Megapodius*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus* (most), *Lagopus*, *Bonasa*, *Pedioecetes* (6 legs), *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Lophortyx* (4 legs), *Alectoris*, *Perdix* (3 legs), *Gennaeus*, *Gallus*, *Phasianus*, *Pavo*, *Numida*, *Meleagris* and *Opisthocomus*.

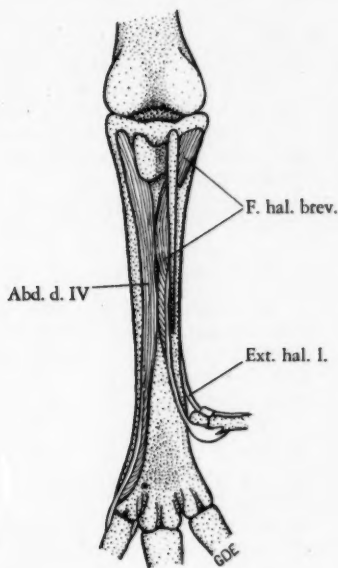
In only *Lagopus mutus*, *Bonasa* and *Tympanuchus* the F. dig. 1. traverses the hypotarsus in a groove which is not roofed over with bone as in the other forms examined.

*M. flexor perforans et perforatus digiti II* (F. p. et p. d. II)

*Description for Dendragapus* (Figs. 1-3, 9, 16-19).—Most of this muscle is superficial on the posterolateral side of the shank. The origin is partly fleshy from the external condyle of the femur distal to the origin of the P. ext. M. gas., from the underlying Bic. loop, and the bellies of the F. p. et p. d. III and Per. long. The belly extends over about the proximal two-thirds of the shank. Along the posterior edge of the muscle there is an ossified tendon beginning a little above the middle of the shank and extending almost to the Tib. cart. Near the base of the second digit the tendon perforates that of the Flex. per. d. II and inserts mainly on the distal end of the basal phalanx and the proximal end of the second phalanx (Fig. 9). Shortly before its insertion the tendon is perforated by the deep flexor. There is a sesamoid in the mid-tarsal region.



Figs. 10, 11 and 12.—Blue grouse (*Dendragapus obscurus*). 10. (Upper left)—Posterior view of proximal end of left shank showing deepest muscles. 11. (Lower left)—Anterior view of left foot showing intrinsic muscles. 12. (Lower right)—Posterior view of left foot showing intrinsic muscles.



**Comparison.**—Variation in the belly of the F. p. et p. d. II was noted as follows: in many forms it is undivided, but in others there is a smaller distal head arising from the posterior edge of the Per. long. and the anterior edge of the F. p. et p. d. III. This joins with the anterior edge of the main tendon about midway the shank or a little below.

Belly single: *Leipoda*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Bonasa*, *Tympanuchus* and *Opisthocomus*.

Intermediate: *Lagopus*, *Canachites*, *Pedioecetes*, *Centrocerus*, *Oreortyx*, *Lophortyx* and *Colinus*.

Two heads: *Megapodius*?, *Alectoris*, *Perdix*, *Gennaeus*, *Gallus*, *Phasianus*, *Pavo*, *Numida* and *Meleagris*.

The belly in *Opisthocomus* is much shorter than in any other form examined, terminating about .36 shank. In one leg of *Perdix* the distal head forms a separate tendon before joining the main tendon. In one leg of *Bonasa* the tendon of the F. p. et p. d. II has no connection with the second digit, but inserts on the joint capsule between the bases of digits two and three. In a few legs of *Meleagris* there is a strong vinculum connecting the tendon of the Flex. per. d. II and that of the F. p. et p. d. II a short distance above the base of the second toe.

Sesamoids in the F. p. et p. d. II were noted as follows:

Both sesamoids present: *Leipoa*, *Ortalis vetula* (1 leg), *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes* (4 legs), *Tympanuchus*, *Centrocerus*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.)

Sesamoid in shank only: *Crax* (1 leg), *Penelope* (ad ♂), *Ortalis vetula* (1 leg), *Pipile* (1 leg) and *Oreortyx*.

Sesamoid in tarsus only: *Pedioecetes* (juv.) and *Gallus* (leghorn; Cornish fowl; silky fowl, ♂; jungle fowl).

No sesamoids present: *Megapodius* (juv.), *Crax* (1 leg), *Ortalis canicollis*, *Penelope* (ad. ♀), *Pipile* (1 leg), *Lophortyx*, *Colinus*, *Alectoris*, *Gallus* (silky fowl, ad. ♀), *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

#### *M. flexor perforans et perforatus digiti III* (F. p. et p. d. III)

*Description for Dendragapus* (Figs. 1-4, 9, 16-19).—Proximally this muscle is partly visible between the F. p. et p. d. II and the Per. long. The origin is largely fleshy from the patellar tendon, the underlying anterolateral region of the tibial crest and from the adjacent lateral arm of the Bic. loop. The belly is strongly attached to the F. p. et p. d. II and Per. long. and terminates a little below the middle of the shank. Along much of the distal half of the shank the tendon is ossified. It passes the Tib. cart. enclosed in the sheath-like tendon of the Flex. per. d. III. The tendon is again ossified for a considerable distance along the posterior side of the tarsometatarsus. Opposite the proximal phalanx of Digit III it perforates the tendon of the Flex. per. d. III, and near the distal end of the proximal phalanx is perforated by the tendon of the deep flexor (Fig. 9). Insertion is on the distal end of Phal. II and the proximal end of Phal. III.

*Comparison*.—The belly is relatively shortest in *Megapodius*, *Alectoris*, *Leipoa* and *Phasianus*, limited to much less than the proximal half of the shank; longest in *Ortalis* and *Opisthocomus*, extending over about the proximal three-fifths; all other forms are intermediate.

Sesamoids in the F. p. et p. d. III were noted as follows:

Both sesamoids present: *Crax*, *Ortalis vetula* (1 leg), *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocerus*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.)

Sesamoid in shank only: *Leipoa*, *Penelope*, *Ortalis vetula* (1 leg), *Ortalis canicollis*, *Pipile* and *Oreortyx*.

Sesamoid in tarsus only: *Gallus*.

No sesamoids present: *Megapodius* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

In *Opisthocomus* only the vinculum between the F. p. et p. d. III and the Flex. per. d. III is absent.

*M. flexor perforatus digiti II* (Flex. per. d. II)

*Description for Dendragapus* (Figs. 3, 4, 9, 16-19).—This deeply situated muscle lies directly posterior to the belly of the F. dig. 1. and lateral to the F. hal. 1. At the proximal end it is divided by the tendon of insertion of the Bic. fem., forming two poorly-defined heads. The medial head arises partly tendinous from the *Reg. intercon.* in common with the medial heads of the Flex. per. d. IV and Flex. per. d. III. The short lateral head arises partly tendinous from the region of the *Caput fibulae* in common with the lateral head of the Flex. per. d. IV. The proximal end of the belly is also strongly attached to the heavy tendon arising from the *Caput fibulae* and receiving the tendon of insertion of the ambiens. The belly of the Flex. per. d. II is closely fused on the medial side to the medial head of the Flex. per. d. III and on the anterolateral edge to the belly of the Flex. per. d. IV and the lateral head of the Flex. per. d. III. The belly ends shortly above the tibial cartilage. Insertion is mainly on the posterolateral edge of the proximal end of Phal. I, Dig. II; the tendon is perforated by that of the F. p. et p. d. II near the base of the proximal phalanx. There is a long sesamoid in the shank and another in the tarsus.

*Comparison*.—Very uniformly developed in all except *Opisthocomus* in which the proximal end of the belly of the Flex. per. d. II is directed mainly into the lateral head, and the entire muscle is more laterally situated than in other forms examined.

Sesamoids in the Flex. per. d. II:

Sesamoids in both shank and tarsus: *Leipoa*, *Crax* (1 leg), *Ortalis*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocerus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.)

Sesamoid in shank only: *Crax* (1 leg), *Penelope* and *Pipile*.

Sesamoid in tarsus only: *Gallus*.

No sesamoids present: *Megapodius* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

In *Meleagris* we found a distinct heavy vinculum between the tendon of the Flex. per. d. II and that of the F. p. et p. d. II a short distance above the base of the second toe in four out of thirty-nine specimens; bilateral in only one. In one leg of *Bonasa* the tendon of the Flex. per. d. II gives off two branches near the distal end of the tarsus; the lateral branch inserts as a typical Flex. per. d. II and the medial branch inserts as a typical F. p. et p. d. II.

*M. flexor perforatus digiti III* (Flex. per. d. III)

*Description for Dendragapus* (Figs. 2-4, 7, 9, 16-19).—This mus-

Fig. 13.—European partridge (*Perdix perdix*). Posterior view of left foot showing intrinsic muscles.

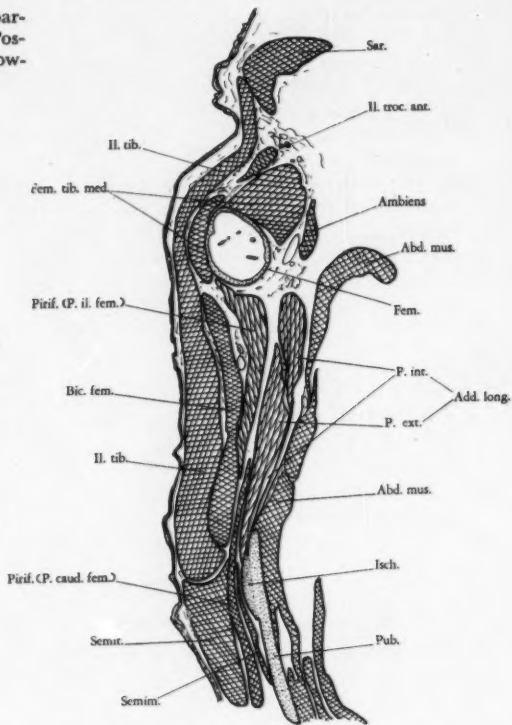
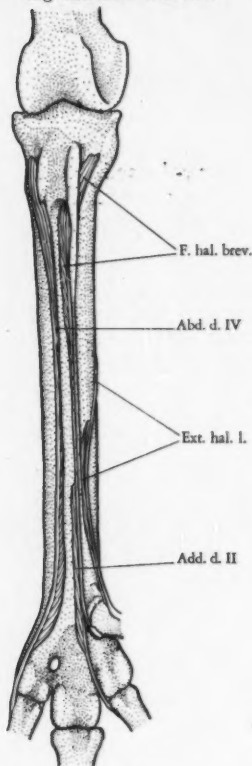


Fig. 14.—Blue grouse (*Dendragapus obscurus*). Cross section of thigh near proximal end.

cle is composed of two distinct heads. The larger medial head arises from the *Reg. intercon.* in common with the medial heads of the *Flex. per. d. II* and *Flex. per. d. IV*. The smaller lateral head is strongly attached to the lateral edge of the belly of the *Flex. per. d. II*. Both have a common origin from the *Caput fibulae* by the tendon which receives the insertion of the ambiens. The medial head forms a definite tendon which is ossified above the point of union with the lateral head; the two fuse a short distance above the Tib. cart. The belly terminates about three-fourths the way down the shank. On the posterior side of the Tib. cart. the tendon of the *Flex. per. d. III* forms a sheath about the more posteriorly situated tendons of the *Flex. per. d. IV* and *F. p. et p. d. III*. Just below the hypotarsus it unites with



the tendon of the Per. long. Insertion is mainly on the distal end of the proximal phalanx and the proximal end of the second phalanx of the third toe. It is clearly perforated by the deep flexors. Just above the distal malleoli of the tarsometatarsus this tendon is connected by a short but strong vinculum with that of the F. p. et p. d. III. The tendon is ossified for most of the length of the tarsus.

*Comparison.*—In some cases the two heads of the Flex. per. d. III unite and only one tendon is formed. In others the medial and lateral heads form separate tendons which unite below.

Lateral head does not form a separate tendon: *Megapodius*, *Leipoa*, *Crax*, *Ortalis*, *Pipile*, *Alectoris*, *Gallus*, *Pavo*, *Numida*, *Meleagris* and *Opisthocomus* (1 spec.).

Two tendons, that of the lateral head short: *Penelope*, *Dendragapus*, *Canachites*, *Pedioecetes*, *Centrocerus*, *Perdix*, *Gennaeus*, *Phasianus* and *Opisthocomus* (2 spec.).

Two tendons, that of the lateral head long: *Lagopus*, *Bonasa*, *Tympanuchus*, *Oreortyx*, *Lophortyx* and *Colinus*.

A sesamoid is present in the shank and another in the tarsus in most forms. In all cases the shank sesamoid was found only in the medial head.

Sesamoids in the Flex. per. d. III varied as follows:

Both sesamoids present: *Leipoa*, *Crax*, *Penelope*, *Ortalis vetula*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocerus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.)

Sesamoid in tarsus only: *Ortalis canicollis*, *Lophortyx*, *Colinus*, *Alectoris*, *Gallus* and *Meleagris* (juv.)

Sesamoids absent: *Megapodius* (juv.), *Numida* and *Opisthocomus*.

The vinculum connecting the tendons of the Flex. per. d. III and the F. p. et p. d. III is present and well developed in all specimens examined except *Opisthocomus* in which it is absent.

#### *M. flexor perforatus digiti IV* (Flex. per. d. IV)

*Description for Dendragapus* (Figs. 2-4, 9, 16-19).—The Flex. per. d. IV is covered on the posterolateral side by the P. ext. M. gas. Origin of the large medial head is fleshy from the *Reg. intercon.* just distal to the insertion of the Acc. semit., in common with the medial head of the Flex. per. d. III. The small lateral head arises by a tendinous sheet from the *Caput fibulae*, external condyle, and lateral arm of the Bic. loop, in common with the lateral head of the Flex. per. d. II. The two heads unite just below the tendon of the Bic. fem. There is a third, smaller head arising from the heavy tendon of origin of the Flex. per. d. II and Flex. per. d. III to which the ambiens tendon is attached. The belly of the Flex. per. d. IV terminates about three-fourths the way down the shank. The tendon of insertion is ossified for a considerable distance in the lower part of the shank. It passes the intertarsal joint ensheathed in the lateral side of the tendon of the Flex. per. d. III as previously described. Toward the distal end of the tarsus the tendon becomes considerably enlarged especially

above the base of the fourth toe. Along the middle portion of the tarsus it is ossified. There are three fairly distinct branches to the tendon of insertion. In addition there is a strong attachment on the medial edge of the base of the proximal phalanx. The most lateral of the three branches inserts on the posterolateral side of the distal end of the proximal phalanx and the proximal end of the second phalanx; the middle branch inserts on the distal end of the second phalanx and the proximal end of the third; the long medial branch inserts mainly on the distal end of the third phalanx and proximal end of the fourth; the tendon of the F. dig. 1. passes between the middle and medial branches.

*Comparison.*—In most forms the small head passing lateral to the biceps tendon is mainly tendinous, but in *Ortalis*, *Lophortyx* and *Opisthocomus* it is somewhat more fleshy. Generally the various branches to the fourth toe are fairly distinct, but there is a considerable amount of fusion in some, especially *Penelope*, *Crax*, and one leg of *Lagopus lagopus*. The tendon of insertion is unusually slender in *Opisthocomus*, especially the branches to the third and fourth phalanges. In one leg of *Opisthocomus* the typically long medial branch is short, terminating at the base of the third phalanx.

The distribution of sesamoids in the Flex. per. d. IV was noted as follows:

Sesamoids present in shank and tarsus: *Leipona*, *Ortalis vetula* (1 leg), *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.)

Sesamoid in shank only: *Crax*, *Penelope*, *Ortalis vetula* (1 leg); *O. canicollis* and *Pipilo*.

Sesamoid in tarsus only: *Gallus*.

Sesamoids absent: *Megapodius*, *Lophortyx*, *Colinus*, *Alectoris*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

*M. flexor hallucis longus* (F. hal. 1.)

*Description for Dendragapus* (Figs. 4, 5, 7, 9, 16-19).—The F. hal. 1. is deeply situated in the shank musculature. The belly is located lateral to the Plan., posterior to the F. dig. 1., and anterior to the Flex. per. d. II. This slender muscle is very much weaker than the F. dig. 1. It arises by a fleshy head from the *Reg. intercon.* and the belly terminates about midway the shank. The tendon passes through the Tib. cart. on the posterolateral side; below this it extends through a groove on the lateral surface of the hypotarsus. Distally it extends diagonally toward the medial side as it passes over the posterior surface of the tendon of the F. dig. 1. A little below the middle of the tarsus the ossified tendon constricts abruptly opposite the vinculum connecting it with the tendon of the F. dig. 1.; below this it extends as a slender tendon which inserts on the ungual phalanx of the hallux. There is also a short fibro-elastic branch connecting with the distal end of the proximal phalanx. Near the base of the hallux the tendon of the F. hal. 1. perforates that of the F. hal. brev. Much of the tendon of the F. hal. 1. is ossified in the region of the shank and again in the posterior sulcus of the tarsometatarsus.

*Comparison.*—In most forms the belly extends about half way down the shank; in *Megapodius*, *Leipoa*, and *Opisthocomus* it is much longer, extending almost to the Tib. cart.

Belly more slender: *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocerus*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Perdix*, *Gennaeus*, *Phasianus*, *Numida* and *Meleagris*.

Intermediate: *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Gallus* and *Pavo*.

Belly stronger: *Megapodius*, *Leipoa* and *Opisthocomus*.

The tendon of the F. hal. 1. in the region of the shank is peculiar in *Numida* in which it is broad and flat proximally.

There is considerable variation in the extent of the vinculum connecting the tendon of this muscle with that of the F. dig. 1. In many forms, such as *Dendragapus*, the vinculum extends only a short distance above the trifurcation of the F. dig. 1. In others, for example *Crax*, the vinculum extends up above the middle of the tarsus.

Vinculum less extensive: *Leipoa*, *Penelope* (♀), *Ortalis canicollis*, *Pipile*, *Dendragapus*, *Pedioecetes*, *Tympanuchus*, *Centrocerus*, *Colinus* (1 leg), *Alectoris* (1 leg), *Numida* (3 legs) and *Opisthocomus*.

Vinculum intermediate: *Megapodius*, *Lagopus*, *Canachites*, *Bonasa*, *Lophortyx* (1 leg), *Colinus* (2 legs), *Alectoris* (4 legs), *Perdix*, *Gallus* (silky fowl, 2 legs; Cornish fowl), *Phasianus* (2 legs), *Pavo* (1 leg), *Numida* (1 leg), and *Meleagris* (juv.).

Vinculum more extensive: *Crax*, *Penelope* (♂), *Ortalis vetula*, *Oreortyx*, *Lophortyx* (3 legs), *Colinus* (2 legs), *Gennaeus*, *Gallus* (leghorn; silky fowl, 2 legs; jungle fowl), *Phasianus* (1 leg), *Pavo* (1 leg) and *Meleagris* (ad.).

In some specimens of the silky fowl the distal end of the tendon of the F. hal. 1. sends a strong bundle of fibers to the tendon of the F. dig. 1. supplying the second digit. This condition was suggested in a specimen of Cornish fowl, one *Phasianus* and *Opisthocomus*, but was not noted in other forms.

In the silky fowl the tendon of the F. hal. 1. bifurcates near the bases of the two halluces and a distinct branch supplies each, although the tendon to the proximal may be somewhat larger.

The accessory fibro-elastic slip from the tendon inserting on the proximal phalanx of the hallux is distinct in most forms, but in some it is rather vague; it was unusually long and distinct in *Opisthocomus*.

Sesamoids in the F. hal. 1. were noted as follows:

Sesamoids present in shank and tarsus: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocerus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

Sesamoid in tarsus only: *Megapodius* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Gallus* and *Numida* (ad.).

Both sesamoids absent: *Numida* (juv.), *Meleagris* (juv.) and *Opisthocomus*.

#### *M. flexor digitorum longus* (F. dig. 1.)

*Description for Dendragapus* (Figs. 1-5, 7, 9, 10, 16-19).—This is the most deeply situated muscle on the posterior and lateral surfaces of the shank. The very small lateral head arises fleshy from the lateral surface of the fibula just proximal to the insertion of the Bic. fem. and is separated from the main belly by the tendon of insertion of

the Bic. fem. The main head arises fleshy from the posterior and lateral surfaces of the fibula and from most of the posterior surface of the shaft of the tibia and terminates just above the proximal end of the tibial cartilage. The proximal end of the main belly is slightly notched just below the insertion of the popliteus to accommodate the passage of nerves and blood vessels. Along most of the length of the belly there is an ossified tendon embedded in the posteromedial surface. After traversing a deep canal in the Tib. cart. the tendon passes through a deep bony canal in the hypotarsus (Fig. 18).

Near the middle of the tarsometatarsus the tendon of the F. dig. I. is connected with that of the F. hal. I. by a vinculum. Opposite the base of the hallux the tendon trifurcates, sending branches to insert mainly on the ungual phalanges of the second, third and fourth digits. The tendon to the second toe has a distinct and sometimes double fibro-elastic slip connecting it with the distal end of the second phalanx and the proximal end of the third. The tendon to the third toe has a similar branch connecting with the distal end of the second and proximal end of the third phalanges; another, sometimes double, branch inserts on the distal end of the third and proximal end of the fourth. The tendon to the fourth toe has a fibro-elastic branch connected with the proximal end of the fourth phalanx and another, sometimes double, branch connected with the distal end of the fourth

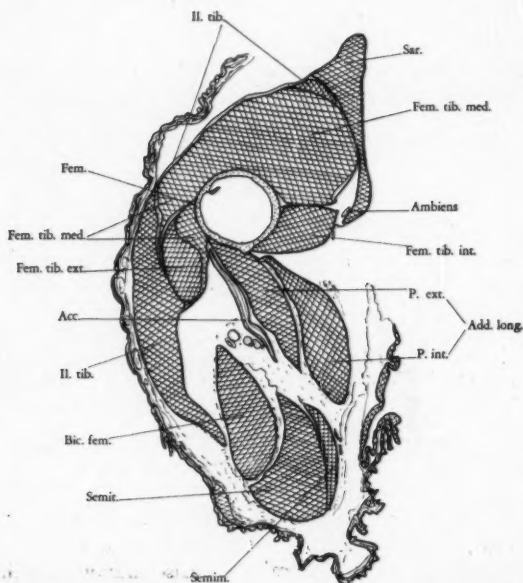


Fig. 15.—Blue grouse. Cross section cut a little below the middle of thigh.

and the proximal end of the fifth. The main tendon of the F. dig. I. is ossified for a considerable distance along the posterior sulcus of the tarsometatarsus.

*Comparison.*—The lateral head of the F. dig. I. is small, about as in *Dendragapus*, in most forms. It is much larger in *Leipoa*; minute in *Ortalis canicollis* and *Crax*; absent in *Penelope*, *Ortalis vetula* and *Pipile*.

The belly of the F. dig. I. is relatively shortest in *Lagopus*, *Oreortyx*, *Lophortyx*, *Colinus* and *Alectoris*, in which it is approximately .75 the length of the shank; longest in *Pipile*, *Centrocercus*, *Tympanuchus*, *Megapodius*, and *Leipoa*, in which the belly extends to .85 shank or more; all others are intermediate.

In *Lagopus mutus*, *Bonasa*, and *Tympanuchus* the tendon of the F. dig. I. traverses a long groove on the posterior side of the hypotarsus; in all other forms examined the groove is roofed over with bone to form a closed canal.

#### VARIATIONS NOTED IN FIBRO-ELASTIC SLIPS

*Second digit.*—Besides the usual accessory attachment near the base of the ungual phalanx, the following have an additional small slip attached near the base of Phal. 2.: *Leipoa* (1 leg), *Lagopus mutus* (1 leg), *Canachites* (2 legs), *Centrocercus* (2 legs), *Oreortyx* (3 legs), *Lophortyx*, *Colinus* (6 legs), *Alectoris* (5 legs), *Perdix* (2 legs) and *Gallus* (silky fowl, 3 legs; Cornish fowl, 1 leg).

*Opisthocomus* differs from all other forms studied in having unusually long and double (right and left) fibro-elastic slips inserting near the base of Phal. 3 and a small single median slip.

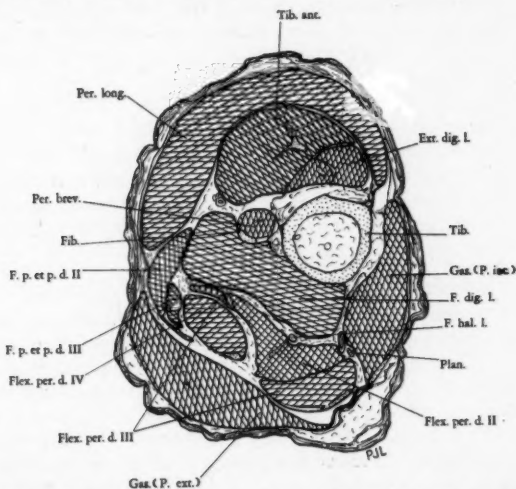


Fig. 16.—Blue grouse. Cross section taken near middle of shank.

*Third digit.*—The proximal slip to the base of Phal. 3 was not found in *Megapodius*. In one leg of *Colinus* there is an additional slip, attached near the base of Phal. 2. The slips to the third digit are unusually long in *Opisthocomus*; the proximal slip is double (right and left) in two legs and undivided in three legs; the distal attachment is divided into right and left slips.

*Fourth digit.*—In many forms an extra slip was found opposite Phal. 2, inserting near the base of Phal. 3. This is often attached to the long branch of the tendon of the Flex. per. d. IV.

Extra slip opposite Phal. 2 present: *Crax*, *Penelope*, *Ortalis*, *Canachites*, *Pedioecetes* (3 legs), *Oreortyx*, *Lophortyx* (5 legs), *Colinus* (4 legs), *Alectoris* (5 legs), *Perdix*, *Gallus* (leghorn; Cornish; silky fowl, 1 leg), *Phasianus* (3 legs), *Pavo*, *Numida*, *Meleagris* (2 legs) and *Opisthocomus*.

Extra slip not noted: *Megapodius*, *Leipoa*, *Pipile*, *Dendragapus*, *Lagopus*, *Bonasa*, *Tympanuchus*, *Centrocercus* and *Gennaeus*.

In *Opisthocomus* the fibro-elastic slips are generally double (right and left). In *Megapodius* and *Leipoa* no slip was found to the base of Phal. 4.

Sesamoids in the F. dig. I. were noted as follows:

Sesamoids in both shank and tarsus: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Perdix*, *Gennaeus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

Sesamoid in tarsus only: *Megapodius* (juv.), *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Numida* (ad.) and *Opisthocomus* (ad.).

Sesamoids absent: *Numida* (juv.), *Meleagris* (juv.) and *Opisthocomus* (juv.).

#### *M. popliteus* (Pop.)

*Description for Dendragapus* (Fig. 10).—This small stout triangular muscle arises mainly fleshy from the posteromedial surface of the head of the fibula. The fibers diverge mediolaterally as the muscle broadens toward the fleshy insertion on the posterior surface of the proximal end of the tibia.

*Comparison.*—The popliteus is present in all specimens and rather uniformly developed. The origin on the fibula is more tendinous in specimens of *Centrocercus* and especially in *Numida*. In *Pavo* and *Meleagris* the muscle is quadrangular in shape with the fibular and tibial attachments about equal in width. *Opisthocomus* shows the reverse of the usual condition in having the tibial attachment narrower than the fibular.

#### SESAMOIDS NEAR PROXIMAL END OF SHANK

In many gallinaceous birds there are three, sometimes four, and rarely five, usually short sesamoids in muscles in the proximal portion of the shank. One of these is located in the common medial head of the Flex. per. d. II and III arising from the *Reg. intercon.*; this is the largest of the five. Another is in the common lateral head of the Flex. per. d. III which is fused with the Flex. per. d. II; this sesamoid is located in the tendinous sheet which is a direct continuation of the tendinous band arising over the joint capsule of the knee and to which the ambiens tendon becomes inserted. Another short sesamoid is some-



times found in the proximal end of the belly of the F. hal. 1. on the medial or anteromedial surface. Another very small sesamoid is sometimes found embedded in the posterior surface of the posterior head of the Tib. ant. just below the knee. A rather large sesamoid is found in many forms embedded in the lateral edge of the Per. long. near the proximal end of the shank; often this is closely applied to the anterior edge of the belly of the F. p. et p. d. III. These five sesamoids were observed as indicated in Table I.

TABLE I.—Variation and occurrence of sesamoids near the proximal end of the shank (numbers refer to single legs)

	In posterior head of Tib. ant.		In lateral edge of Per. long.		In lateral head of Flex. per. d. III		In medial head of Flex. per. d. II and III		In proximal part of F. hal. 1.	
	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent
<i>Leipoa</i>	0	2	0	2	2	0	2	0	2	0
<i>Crax</i>	0	2	0	2	2	0	2	0	0	2
<i>Penelope</i>	0	4	0	4	0	4	0	4	0	4
<i>Ortalis</i>	1	2	0	3	2	1	2	1	0	3
<i>Pipile</i>	0	1	0	1	1	0	0	1	0	1
<i>Dendragapus</i>	3	2	5	0	5	0	5	0	0	5
<i>Lagopus</i>	2	4	5	1	6	0	6	0	4	2
<i>Canachites</i>	2	2	4	0	4	0	4	0	0	4
<i>Bonasa</i>	2	4	0	0	4	0	4	0	0	4
<i>Pedioecetes</i>	6	2 (juv.)	6	2 (juv.)	6	2 (juv.)	6	2 (juv.)	0	8
<i>Tympanuchus</i>	2	0	2	0	2	0	2	0	0	2
<i>Centrocerus</i>	4	0	4	0	4	0	4	0	0	4
<i>Oreortyx</i>	0	4	0	4	0	4	0	0	0	3
<i>Lophortyx</i>	0	5	0	5	0	5	0	5	0	5
<i>Colinus</i>	0	7	0	7	0	7	0	7	0	7
<i>Alectoris</i>	0	4	0	4	0	4	0	4	0	4
<i>Perdix</i>	2	4	6	0	2	4	6	0	6	0
<i>Gennaeus</i>	1	1	2	0	2	0	2	0	2	0
<i>Gallus</i>	0	10	0	10	0	10	0	10	0	10
<i>Phasianus</i>	1	4	3	2	4	1	5	0	0	5
<i>Pavo</i>	0	2	0	2	0	2	0	2	0	2
<i>Numida</i>	0	4	0	4	0	4	0	4	0	4
<i>Meleagris</i>	0	4	2	2 (juv.)	2	2 (juv.)	2	2 (juv.)	1	3
<i>Opisthocomus</i>	0	4	0	4	0	4	0	4	0	4

*M. extensor hallucis longus* (Ext. hal. 1.)

*Description for Dendragapus* (Figs. 6-8, 11, 18, 19).—The Ext. hal. 1. arises fleshy from an extensive area on the anteromedial surface of about the proximal .6 of the tarsometatarsus, the belly extending almost to the base of the hallux. Distally the muscle passes diagonally over the medial side of the tarsometatarsus to the base of the hallux. The tendon extends along the dorsal surface of the hallux to which it is closely connected; the insertion terminates on the ungual phalanx. In some specimens the tendon is ossified for a very short distance (about 2 mm) on the medial surface at about .6 tarsometatarsus. In only two out of seven legs we found a small trace suggesting a short distal head.

*Comparison.*—The main belly of the Ext. hal. 1. is short in *Alectoris*, *Lagopus*, and *Centrocerus*, being confined to about the proximal half or less of the tarsometatarsus. The belly is long in *Crax*, *Penelope*, *Ortalis*, *Pipile* and *Opisthocomus* extending to about .8 tarsometatarsus. All other forms are intermediate.

In many specimens the main belly is attenuated at the point where



the muscle extends over the medial surface of the tarsometatarsus, producing a more or less distinct division into a proximal belly and a distal belly, a condition most clearly observed in *Canachites*, *Pedioecetes*, *Tympanuchus*, *Oreortyx*, *Lophortyx*, *Alectoris*, *Perdix* and *Colinus*.

In *Numida* the belly is unusually broad near the proximal end, extending over most of the anterior surface of the tarsometatarsus.

In many specimens there is a distinct, short, distal head which, when best developed, might justify the name "extensor hallucis brevis." This is most definite in *Crax*, *Penelope*, *Ortalis*, *Pipile* and *Opisthocomus*.

Short head distinct: *Megapodius*, *Leipoa* (1 leg), *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Numida* (1 leg) and *Opisthocomus*.

Short head very weak: *Dendragapus* (2 legs), *Lagopus* (2 legs), *Canachites*, *Bonasa* (2 legs), *Pedioecetes* (3 legs), *Colinus* (1 leg), *Perdix*, *Numida* (4 legs) and *Meleagris* (juv.).

Short head not observed: *Leipoa* (1 leg), *Dendragapus* (5 legs), *Lagopus* (4 legs), *Bonasa* (2 legs), *Pedioecetes* (4 legs), *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Lophortyx*, *Colinus* (7 legs), *Alectoris*, *Gennaeus*, *Gallus*, *Phasianus*, *Pavo* and *Meleagris* (ad.).

In most cases in which the short head is present, the two are more or less fused at the base of the hallux. In *Opisthocomus* they are not connected at this point, the tendon of the long head gliding freely over the short head.

The main head of the Ext. hal. I. shows ossification of the tendon as follows:

Sesamoid present, one center of ossification: *Leipoa*, *Penelope* (3 legs), *Dendragapus* (1 leg), *Lagopus* (2 legs), *Canachites* (3 legs), *Tympanuchus* (1 leg) and *Meleagris* (ad.).

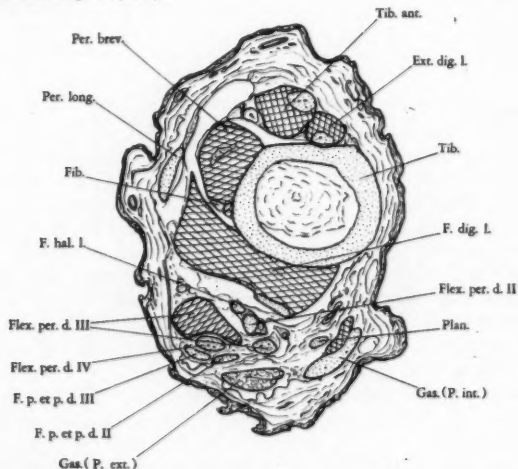


Fig. 17.—Blue grouse. (*Dendragapus obscurus*). Cross section taken near distal end of shank.

Sesamoid present, two centers of ossification: *Lagopus* (2 legs) and *Pedioecetes* (5 legs).

Sesamoid present, three centers of ossification: *Lagopus* (1 leg).

Sesamoid absent: *Megapodius* (juv.), *Crax*, *Penelope* (1 leg), *Ortalis*, *Pipile*, *Dendragapus* (7 legs), *Canachites* (1 leg), *Bonasa*, *Pedioecetes* (2 legs, juv.), *Tympanuchus* (1 leg), *Centrocerus*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Perdix*, *Gennaeus*, *Gallus*, *Phasianus*, *Pavo*, *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

In the Tetraonidae sesamoids in the Ext. hal. I. are so small that they can be demonstrated only by partly drying the legs and examining under a dissecting binocular microscope. In the silky fowl the Ext. hal. I. is attached only to the lower hallux and has no connection with the longer upper hallux.

*M. extensor proprius digiti III* (Ext. pro. d. III)

*Description for Dendragapus* (Figs. 8, 11, 19).—The origin is fleshy from the anterior surface of somewhat less than the distal half of the tarsometatarsus. The short, flat tendon inserts on the antero-proximal edge of the basal phalanx of the third digit.

*Comparison.*—The length of the Ext. pro. d. III shows considerable variation.

Belly long, beginning in proximal fourth of tarsus: *Leipoa* and *Opisthocomus*.

Belly begins in second fourth of tarsus: *Megapodius*, *Crax*, *Penelope* (2 legs), *Bonasa* (1 leg), *Colinus* (1 leg), *Gallus* (leghorn; Cornish fowl; jungle fowl, 1 leg) and *Numida*.

Belly begins in third fourth of tarsus: *Penelope* (2 legs), *Ortalis*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa* (3 legs), *Pedioecetes*, *Tympanuchus*, *Centrocerus*, *Oreortyx*, *Lophortyx*, *Colinus* (8 legs), *Alectoris* (2 legs),

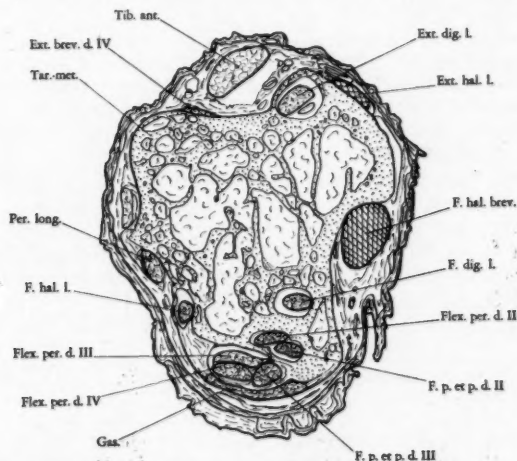


Fig. 18.—Blue grouse. Cross section through hypotarsus.

*Perdix*, *Gennaeus*, *Gallus* (silky fowl; jungle fowl, 1 leg), *Phasianus* (4 legs), *Pavo* and *Meleagris*.

Belly short, confined to distal fourth of tarsus: *Alectoris* (2 legs) and *Phasianus* (1 leg).

The Ext. pro. d. III is most powerfully developed in *Opisthocomus*, the belly usually extending above the insertion of the Tib. ant. on the lateral side. The tendon is narrow and embedded in the middle of the anterior surface, giving the muscle a bipinnate appearance. The muscle is almost vestigial in *Alectoris*, the belly being very thin and poorly developed.

In two specimens of *Numida* (one leg of each) there is a minute muscle lying on the medial side of the Ext. pro. d. III, the two enclosed in a single fibrous membrane. This muscle begins a little below the middle of the tarsus, the belly measuring about 1 x 15 mm. Distally the delicate tendon inserts near the anterolateral edge of the basal phalanx of the second digit and might be considered an "extensor brevis digiti II." However the position of this muscle agrees with the description of the "Extensor brevis digiti III" of Gadow (1891: 199).

*M. extensor brevis digiti IV* (Ext. brev. d. IV)

*Description for Dendragapus* (Figs. 1, 8, 11, 19).—This small muscle arises fleshy from the anterolateral surface of a little more than the proximal half of the tarsometatarsus. The short, flat tendon runs through a bony canal in the outer intermetatarsal space and inserts on the posteromedial side of the proximal phalanx of the fourth digit. A sesamoid is present in the tendon.

*Comparison*.—There is considerable variation in the relative length of the belly.

Belly limited to proximal half of tarsus: *Lagopus*, *Canachites* (3 legs) and *Bonasa*.

Belly intermediate: *Dendragapus*, *Canachites* (1 leg), *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx* (2 legs), *Perdix* and *Gallus* (leghorn).

Belly extends to intermetatarsal canal or nearly so: *Megapodius*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Oreortyx* (1 leg), *Lophortyx*, *Colinus*, *Alectoris*, *Gennaeus*, *Gallus* (silky fowl, Cornish fowl; jungle fowl), *Phasianus*, *Pavo*, *Numida*, *Meleagris* and *Opisthocomus*.

The belly begins almost at the proximal end of the tarsus except in *Opisthocomus* in which the upper end is located at about .3 tarso-metatarsus.

In most forms the bellies of the Ext. brev. d. IV and Abd. d. IV are rather widely separated near the distal end of the tarsus; in *Megapodius* and *Opisthocomus* they are adjacent.

Ossification of the tendon of the Ext. brev. d. IV was noted as follows:

Sesamoid present: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes* (5 legs), *Tympanuchus*, *Centrocercus*, *Perdix*, *Gennaeus*, *Phasianus* (3), *Pavo* and *Meleagris* (ad.).

Sesamoid not observed: *Megapodius*, *Pedioecetes* (juv.), *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Phasianus* (2), *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

*M. abductor digiti II* (Abd. dig. II)

*Description for Dendragapus* (Figs. 6-8, 11, 19).—A short, fleshy muscle extending along about the distal two-fifths of the medial surface of the Tar. met. The origin is from the medial surface of Met. II and from Met. I; insertion is by a short tendon on the posteromedial surface of the base of Phal. I, Dig. II.

*Comparison.*—There is great variation in the relative length of the muscle. It is longest in *Megapodius* and *Leipoa*, extending along about the distal three-fourths of the tarsus; somewhat shorter in *Gallus* and *Opisthocomus*; shortest in *Ortalis vetula*, *Bonasa*, *Gennaeus*, *Pavo*, *Phasianus* and *Meleagris*, limited to about the distal third of the tarsus; limited to about the distal third to half of the tarsus in other forms examined.

Generally the muscle is situated entirely on the medial side of the tarsometatarsus, but in *Megapodius*, *Leipoa* and *Gallus*, it extends laterally onto the anterior surface proximally; there is a tendency toward this in *Numida* and *Opisthocomus*.

*Opisthocomus* differs from all other forms examined in that the insertion is mainly on the posterior surface of Phal. I, the attachment extending from the base almost to the distal end of this phalanx; action is a combination of abduction and flexion of the index digit.

*M. flexor hallucis brevis* (F. hal. brev.)

*Description for Dendragapus* (Figs. 5-7, 9, 10, 18, 19).—This is the strongest of the short toe muscles and arises from an extensive area on the posteromedial surface of the tarsometatarsus. At the proximal end the belly is very broad and extends medially beneath the bony bridge formed by the ossification of part of the Gas. tendon extending from the hypotarsus to the shaft of the tarsometatarsus (Fig. 12). Proximally the belly lies on the medial surface of the hypotarsus. Fleshy fibers extend almost to Met. I. The tendon becomes much broader at the insertion on the posteroproximal edge of Phal. I, Dig. I, at which point it is perforated by the tendon of the F. hal. I.

*Comparison.*—In all forms examined the muscle extends almost up to the proximal end of the tarsometatarsus. Variations in the length of the belly of the F. hal. brev. were noted as follows:

Belly confined to about proximal half or less of the tarsometatarsus: *Lagopus*, *Canachites*, *Bonasa* (3 legs), *Perdix* (1 leg), *Gennaeus*, *Gallus* (silky fowl ♂) and *Phasianus* (2 legs).

Intermediate: *Dendragapus*, *Bonasa* (1 leg), *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx* (1 leg), *Lophortyx*, *Alectoris* (1 leg), *Perdix* (4 legs), *Gallus* (silky fowl, ♀), *Phasianus* (1 leg), *Numida* (3 legs) and *Meleagris*.

Belly extends along about proximal two-thirds or more of the tarsometatarsus: *Megapodius*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Oreortyx* (2 legs), *Colinus*, *Alectoris* (3 legs), *Gallus* (leghorn; Cornish fowl; jungle fowl), *Pavo*, *Numida* (2 legs) and *Opisthocomus*.

The F. hal. brev. is extremely weak and attenuated in *Lagopus*. In *Opisthocomus* the muscle is powerfully developed.

In *Megapodius*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, and *Pipile* the

proximal end of the strongly developed belly wraps sheath-like around the tendon of the F. dig. I.; in most forms the posteroproximal part of the belly is shallowly grooved to receive the tendon of the F. dig. I. In *Opisthocomus* the tendon of the F. dig. I. just below the hypotarsus is ensheathed by the F. hal. brev. medially and the Add. d. II laterally.

The tendon of insertion is divided in *Megapodius* and *Leipoa*, less distinctly so in the latter. In four legs of the silky fowl there was great variation in the insertion: in two the insertion is mainly on the base of the lower hallux, but in one of these there is a diffuse connection with the upper hallux; in one the insertion appears to be divided almost equally between the two, but there is no definite branching; in one there is a strong, rather diffuse connection with the upper hallux but the main insertion is near the distal end of the tarsometatarsus, and with a definite connection with the joint capsule of the second and third toes, without any attachment to the lower hallux. In all forms the tendon is clearly perforated by the F. hal. I. Sesamoids in the F. hal. brev. were noted as follows:

Sesamoid present: *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Pedioecetes* (3 legs), *Tympanuchus*, *Perdix*, *Gennaeus*, *Phasianus* (1 leg), *Pavo* and *Meleagris* (ad.).

Sesamoid absent: *Megapodius* (juv.), *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes* (4 legs), *Centrocercus*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Gallus*, *Phasianus* (4 legs), *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

#### *M. adductor digiti II* (Add. d. II)

*Description for Perdix* (Figs. 13, 20).—The origin is fleshy from

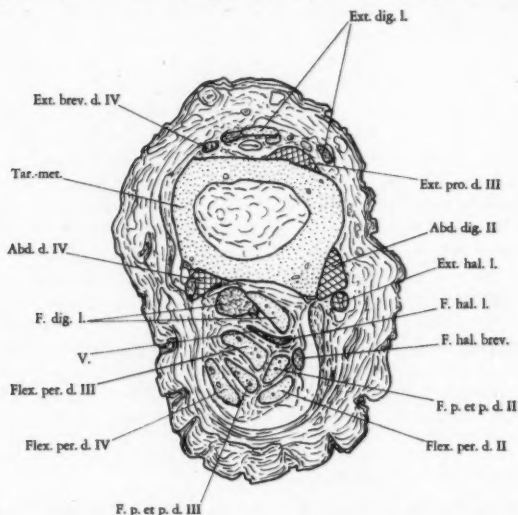


Fig. 19.—Blue grouse. Cross section of tarsus taken a short distance above base of hallux.

the middle line of the posterior surface of the Tar. met., beginning a little below the middle of that bone. The belly is broad distally and narrow proximally. The short tendon inserts on the medial edge of the base of Phal. I, Dig. II.

*Comparison.*—In all members of the Family Tetraonidae examined, the Add. d. II is absent; it is present in all other forms, although we found it lacking on the left side of both specimens of *Odontophorus*. The occurrence of this muscle in a hybrid Ring-necked Pheasant X Blue Grouse described by Hudson (1955) indicates that its presence is a dominant characteristic.

There is considerable variation in the relative length of the muscle compared to the length of the tarsus.

Muscle long, reaching hypotarsus: *Opisthocomus*.

Intermediate: *Megapodius*, *Leipoa*, *Crax*, *Penelope*, *Ortalis*, *Pipile*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris* (1 leg), *Perdix*, *Gallus*, *Pavo* and *Numida*.

Muscle short, confined to about distal third or less of tarsus: *Alectoris* (3 legs), *Gennaues* (very weak), *Phasianus* and *Meleagris*.

In *Gennaues* and *Pavo* we could find no direct connection with the second toe. The very weak tendon appeared to terminate near the joint pulley.

In *Opisthocomus* only the tendon of insertion is very long, the belly being confined to about the proximal half of the tarsus. In no case did we find a sesamoid in this muscle.

#### *M. lumbricalis* (Lumb.)

*Description for Dendragapus.*—This muscle is represented by a single small, partly fleshy slip arising from the anterior surface of the

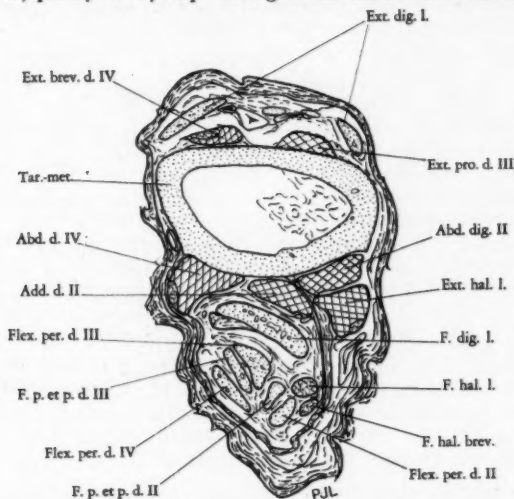


Fig. 20.—European partridge (*Perdix perdix*). Cross section of tarsus taken a short distance above base of hallux.



trifurcated tendon of the F. dig. I. and extending distally along the branch supplying the third toe. It inserts mainly on the fibrocartilaginous joint pulley of the third toe. The muscle is generally feebly developed and the power of contraction is probably very limited.

*Comparison.*—In most forms the lumbricalis is weak but clearly discernible as in *Dendragapus*; it is weaker and more vestigial in *Lagopus*, *Canachites*, *Oreortyx* (2 legs), *Alectoris*, *Gennaeus*, *Gallus*, and *Numida*; apparently absent in *Pavo*.

*Opisthocomus* differs radically from all the others in that the muscle is very long, strongly developed, and divided into two distinct bellies. The posterolateral belly arises from the lateral surface of the tendon of the F. hal. I. beginning above the vinculum. It inserts on the joint pulley for the fourth digit. The anteromedial belly arises in about the usual position from the anterior surface of the tendon of the F. dig. I. beginning a little above the vinculum. Insertion is mainly on the base of the joint pulley of the third toe. In one specimen the anteromedial belly has a small and fairly separable slip on the lateral side.

#### *M. abductor digiti IV* (Abd. d. IV)

*Description for Dendragapus* (Figs. 1, 3-5, 9, 12, 19).—The Abd. d. IV arises fleshy from a long line on the posterolateral surface of the tarsometatarsus beginning on the lateral side of the hypotarsus and extending almost to the base of the fourth toe. The short tendon inserts on the lateral side of the base of Phal. I, Dig. IV.

*Comparison.*—The muscle is most strongly developed in *Megapodius*, *Leipoa*, and *Opisthocomus*; weakest in *Lagopus*, *Oreortyx*, *Alectoris*, *Gennaeus*, *Gallus*, *Phasianus*, and *Numida*; intermediate in all others.

In *Megapodius* the belly is narrow proximally and broader distally; the width little changed throughout in *Leipoa*. In the *Cracidae*, *Gennaeus* and *Pavo*, the belly is distinctly narrowed near the middle. In most forms the belly is broader proximally and narrower distally.

The presence of a sesamoid in the Abd. d. IV was noted as follows:

Sesamoid present: *Leipoa*, *Crax*, *Penelope* (♂), *Ortalis vetula*, *Pipile*, *Perdix* (5 legs), *Gennaeus*, *Phasianus* (2 legs), *Pavo* and *Meleagris* (ad.).

Sesamoid absent: *Megapodius* (juv.), *Penelope* (♀), *Ortalis canicollis*, *Dendragapus*, *Lagopus*, *Canachites*, *Bonasa*, *Pedioecetes*, *Tympanuchus*, *Centrocercus*, *Oreortyx*, *Lophortyx*, *Colinus*, *Alectoris*, *Perdix* (1 leg), *Gallus*, *Phasianus* (3 legs), *Numida*, *Meleagris* (juv.) and *Opisthocomus*.

#### *M. adductor digiti IV* (Add. d. IV)

Although Hudson (1937:58) reported this rudimentary muscle in a single specimen of ring-necked pheasant (*Phasianus colchicus*), we failed to find it in any of the Galliform birds examined.

#### SUPERNUMERARY SESAMOIDS OF THE PELVIC LIMB

There is considerable variation in the occurrence of sesamoids in the shank and foot (Table II). The Megapodiidae have practically



all of these well-developed although the one juvenile specimen of *Megapodius* was apparently too young to have them formed. In the Cracidae there is a tendency toward reduction in the number of sesamoids of the shank muscles in the region of the tarsus; although *Ortalis vetula* has eight, the higher numbers, nine and ten, found in some of the Tetraonidae and Phasianidae apparently do not occur here.

Variation in these sesamoids in the Tetraonidae is slight and the maximum numbers, or nearly so, occur in all forms examined.

There is a striking difference within the Family Phasianidae between the genera *Lophortyx*, *Colinus* and *Alectoris* and other genera such as *Oreortyx*, *Perdix* and various types of pheasants. The great reduction in sesamoids in *Lophortyx*, *Colinus*, and *Alectoris* seems to be an important modification. As noted in Table II only three were found in these birds with the exception of one specimen of *Alectoris* in which there were four. Not only the same number occurs, but the same ones are present; it seems unlikely that this could be due to convergence.

*Gallus* shows great reduction in the sesamoids since usually none and not more than one are present in the shank, although the number is fairly large in the region of the tarsus; however, here they are present in the long shank muscle tendons only and none were found in the short foot muscles. Our specimen of the red jungle fowl agrees fully with the domestic fowl in this respect, suggesting that this is an original condition and the sesamoids have not been eliminated by selective breeding.

The maximum reduction of sesamoids is found in *Numida* and *Opisthocomus*: *Numida* with only two, in the deep flexor tendons in the region of the tarsus, and *Opisthocomus* with only one, in the tendon of the F. dig. I.

In examining specimens for sesamoids it is necessary that the birds be mature or nearly so and in small forms, such as quails and partridges, the short muscles in the region of the tarsus may have minute sesamoids which are not easy to demonstrate unless the specimen is at least partly dried and examined under a dissecting microscope.

The only muscles in the pelvic limb below the knee that do not have sesamoids in any of these gallinaceous birds are the popliteus in the shank and the Ext. pro. d. III, Abd. dig. II, Add. d. II and lumbricalis in the region of the foot.

The occurrence of sesamoids in gallinaceous birds must be considered a primitive characteristic of the group since they are well represented in all families with the possible exception of the Numididae, and *Opisthocomus* which is doubtfully associated with the order.

We are unable to offer any explanation of the possible adaptive significance of these supernumerary sesamoids. They are found in some highly terrestrial forms such as *Perdix* and *Oreortyx* but are greatly reduced in number in *Colinus* and *Alectoris*, closely related forms of generally similar habits.



TABLE II (Continued)

<b>Short proximal sesamoids in shank:</b>															
			(1)	(3)	(2)	(2)	(2)	X	X		(2)	(1)			
Post. head of Tib. ant.				X	X	(5)	X	X	X		X	X	(3)	X	X
Per. long. (lat.)															
Lat. head of Flex. per. d. III	X	X	X	X	X	X	X	X	X		(2)	X	X	X	X
Med. head of Flex. per. d. III	X	X	X	X	X	X	X	X	X			X	X	X	X
F. hal. I.	X				(4)						X	X	X	X	X
Ext. hal. I.	X	(3)		(1)	X	(3)		X	(1)		X	X		X	X
Ext. brev. d. IV	X	X	X	X	X	X	X	X	X		X	X	(3)	X	X
F. hal. brev.	X	X	X	X	X	X				(3)	X	X	(1)	X	X
Abd. d. IV	X	X	(♂)	X	X						(5)	(2)	X	X	X

## SUMMARY (maximum nos.)

Seamoids in shank muscles																								
In tarsus																								
In shank																								
1	15	13	10	16	10	11	18	19	18	18	18	15	0	0	0	19	19	1	18	18	0	18	0	
2	7	6	4	8	5	4	9	9	9	9	8	6	3	3	4	10	9	8	10	9	2	9	1	
Short foot muscles with seamoids																								
0	4	3	4	3	2	3	2	2	2	1	3	3	1	0	0	0	3	3	3	0	4	0	0	
3	26	22	18	27	17	18	29	30	29	28	30	27	21	3	3	4	32	31	9	31	30	2	31	1
Total																								

\* Sesamoid located in shank

**## Sesamoid located in tarsus**

† *Callipepla squamata* agrees with *Lophortyx* and *Colinus*; *Odontophorus guttatus* differs only in having a sesamoid in the tendon of the E. dig. 1. in the tarsus.

TABLE III.—Principal modifications of pelvic limb muscles in families of Galliformes

	<i>Megapodiidae</i>	<i>Cracidae</i>	<i>Tetraonidae</i>	<i>Phasianidae</i>	<i>Numida</i>	<i>Meleagris</i>	<i>Ophthorcomus</i>
II. troc. med.	Clearly discernible	Clearly discernible	Clearly discernible	Clearly discernible	Clearly discernible	Clearly discernible	Fused with II. troc. ant.
Ambiens tendon	Typical	Typical	Typical	Typical	Typical	Typical	Disappears at knee
P. caud. fem. of Piril.	Present	Present	Present	Present (No caudal attachment in <i>Pavo</i> )	Present	Absent	Present
Semit.	Origin partly from caudal vertebrae	Same	Same	Same	Same	Same	From ilium only
Semin.	Origin most posterior	Origin most anterior	Intermediate	Intermediate	Most anterior	Intermediate	Most posterior
Obt. int.	Origin partly from ventrolateral surface of ilium	Same	Same	Same	Same	Same	No
P. int. of Add. long.	Insertion tendinous	Same	Fleshy	Usually tendinous	Tendinous	Same	Fleshy
E. dig. I.	Tendon bifurcates	Same	Same	Same	Same	Same	Trifurcates
Per. long.	Belly broad and long	Same	Same	Same	Same	Same	Short, narrow, lateral
P. int. of Gas.	Extends around front of knee	Same	Same	Same	Same	Same	No
P. ext. and P. int. of Gas. with separate tendons above fusion	Yes in <i>Megapodius</i>	No	Yes	Yes, except <i>Gallus</i>	No	Yes?	No
F. p. et p. d. II	Length of belly typical	Same	Same	Same	Same	Same	Very short
Vinculum	Connects tendons of Flex. per. d. III and F. p. et p. d. III	Same	Same	Same	Same	Same	Absent

TABLE III (Continued)

	<i>Megapodiidae</i>	<i>Cracidae</i>	<i>Tetraonidae</i>	<i>Phasianidae</i>	<i>Numida</i>	<i>Meleagris</i>	<i>Ophithorcomus</i>
Flex. per. d. II	Main head medial to tendon of Bic. fem.	Medial	Medial	Medial	Medial	Medial	Lateral
F. hal. I.	Belly long	Belly short, ending about midway shank	Same	Same	Same	Same	Belly long
Ext. hal. I., short head	Distinct (Except one leg of <i>Leipoa</i> )	Distinct	Absent or vestigial	Absent or vestigial	Vestigial (usually)	Absent or vestigial	Distinct
Abd. dig. II insertion	On lateral side of base of Phal. I	Lateral	Lateral	Lateral	Lateral	Lateral	Mainly on posterior side
Add. d. II	Present	Present	Absent	Present	Present	Present	Present
Tendon of Add. d. II	Short	Short	Absent	Short	Short	Short	Both muscle and tendon long
F. hal. brev. belly	Ensheathes tendon of F. dig. I.	Ensheathes	Does not ensheath tendon	Same	Same	Same	Same
F. hal. brev. tendon	Divided	Not divided	Not divided	Not divided	Not divided	Not divided	Not divided
Lumb.	One feeble belly	Same	Same	Same	Same	Same	Long, two bellies
<i>Sesamoids in shank muscles</i>							
In shank	1 and 15 (1 in juv. <i>Megapodius</i> )	9, 13, 15 or 16	15 - 19	0, 1, 15, 17 - 19	0	17 - 18	0
In tarsus	2 and 7 (2 in juv. <i>Megapodius</i> )	4, 5, 6 or 8	8 or 9	3, 4, 6, 8, 9 or 10	2	9	1
Short muscles of foot with sesamoids	0 and 4 (none in juv. <i>Megapodius</i> )	2, 3 or 4	1, 2 or 3	0 - 3	0	4	0
Total	3 and 26 (3 in juv. <i>Megapodius</i> )	16 - 27	27 - 30	3, 4, 8, 9, 21, 26 - 32	2	30 - 31	1

TABLE IV.—Principal differences noted within the family Megapodiidae

	<i>Megapodius</i> (Juv.)	<i>Leipoa</i>
Sartorius	Narrow	Broad
Per. long.	Belly shorter, not fleshy to bifurcation	Belly longer, fleshy to bifurcation
Vinculum between F. hal. I. and F. dig. I.	More extensive	Less extensive
Ext. pro. d. III	Belly shorter, does not extend up to Tib. ant. insertion	Belly longer, extends up to Tib. ant. insertion
Bellies of Ext. brev. d. IV and Abd. d. IV	Adjacent near lower end of tarsus	Not adjacent at any point
Add. d. II	Extends above middle of tarsus	Extends up to middle of tarsus
Abd. d. IV	Strongly developed, especially at distal end	Weaker, especially at distal end
Sesamoids in shank muscles		
In shank	1	15
In tarsus	2	7
Short muscles of foot with sesamoids	0	4
Total	3	26

TABLE V.—Principal differences noted within the family Cracidae

	<i>Crax</i>	<i>Penelope</i>	<i>Ortalis</i>	<i>Pipile</i>
Glut. med. et. min. origin	More extensive	More	Less extensive	Less
Fem. tib. ext.	Extends well above middle of femur	Shorter	Shorter	Shorter
P. caud. fem. of pirif.	Origin by a short tendon	No tendon of origin	No tendon	No tendon
Fusion of P. caud. fem. with P. il. fem.	Over one inch posterior to femur	Closer to femur	Closer to femur	Closer to femur
Belly of P. caud. fem. of Pirif.	Narrower, less than $\frac{1}{2}$ width of P. il. fem.	Broader, more than $\frac{1}{2}$ width of P. il. fem.	Same	About half the width of P. il. fem.
Isch. fem.	Shorter	Shorter	Shorter	Longer, extending farther back on ischium

TABLE V (Continued)

	<i>Crax</i>	<i>Penelope</i>	<i>Ortalis</i>	<i>Pipile</i>
P. int. of Add. long.	About twice bulk of P. ext.	Less than twice bulk of P. ext.	Same	About twice bulk of P. ext.
Ext. dig. I. bifurcation	Well below middle of tarsus	Same	About midway tarsus	Well below middle of tarsus
Sesamoid of E. dig. I. in foot	Both branches of bifurcation ossified	Ossified	Ossified	Medial branch not ossified
Per. long. sesamoid	Present	Absent	Present	Absent
Gastrocnemius sesamoid	Absent	Absent	Present in P. ext. of <i>O. vetula</i> only	Absent
Plantaris sesamoid	Absent	Absent	Present	Absent
F. p. et. p. d. II sesamoids				
In shank	Present in 1 leg; absent in 1 leg	Present in 1 ♂; Absent in 1 ♀	In <i>O. vetula</i> only	Present in 1 leg; absent in 1 leg
In tarsus	Absent	Absent	In one leg of <i>O. vetula</i> only	Absent
F. p. et. p. d. III sesamoid in tarsus	Present	Absent	Present in 1 leg of <i>O. vetula</i> only	Absent
Flex. per. d. II sesamoid in tarsus	Present in 1 leg; absent in 1 leg	Absent	Present	Absent
Flex. per. d. III	Only one tendon	Both heads form tendons	Only one tendon	Only one tendon
Flex. per. d. III sesamoid in shank	Present	Present	Present in <i>O. vetula</i> ; absent in <i>O. canicollis</i>	Present
Vinculum between F. hal. I. and F. dig. I.	Extends above middle of tarsus	Extends above middle of tarsus in ♂; shorter in ♀	Extends above middle of tarsus in <i>O. vetula</i> ; shorter in <i>O. canicollis</i>	Does not extend up to middle of tarsus
Ext. hal. I. sesamoid	Absent	Present in 3 legs; absent in one	Absent	Absent
Ext. pro. d. III	Extends above middle of tarsus	Extends above middle of tarsus in ♂; shorter in ♀	Extends up to middle of tarsus or a little below	Same
Abd. d. IV sesamoid	Present	Present in ♂; absent in ♀	Present in <i>O. vetula</i> ; absent in <i>O. canicollis</i>	Present
Sesamoids in shank muscles				
In shank	12 or 13	9 or 10	( <i>vetula</i> ) 15 or 16	( <i>canicollis</i> ) 10
In tarsus	5 or 6	4	5 or 8	5
Short muscles of foot with sesamoids	3	4 (2 of these may be absent)	3	2
TOTAL	20-22	16-18	23-27	17
				17 or 18



TABLE VI.—Principal differences noted within the family Tetraonidae

[illegible]

TABLE VI (cont.)

	<i>Dendragapus</i>	<i>Lagopus</i>	<i>Canachites</i>	<i>Bonasa</i>	<i>Pediceetes</i>	<i>Tympanuchus</i>	<i>Centrocerus</i>
F. dig. l. tendon in hypotarsus	In bony canal	In bony canal in <i>L.</i> ; in open groove in <i>L. mutus</i>	In bony canal	In open groove	In bony canal (except in 1 juv.)	In open groove	In bony canal
Belly of Ext. hal. l. on medial side of Tar. met.	Not attenuated	Variable; belly usually short	Attenuated; then dilated distally	Not attenuated	Intermediate	Attenuated; then dilated distally	Short, belly ends about midway tarsus
Ext. hal. l. sesamoid	Present in 1 leg; absent in 7	Present	Present in 3 legs; absent in 1	Absent	Present	Present in 1 leg; absent in 1	Absent
Belly of Ext. brev. d. IV	Extends below middle of tarsus, sometimes much below	Ends about midway tarsus or above	Ends about midway tarsus	Ends about a little above	Extends below middle of tarsus, sometimes much below	Extends a little below middle of tarsus	Same
Belly of F. hal. brev.	Extends below middle of tarsus	Ends above middle of tarsus, sometimes far above; very weak	Ends above middle of tarsus	Ends about midway tarsus	Extends below middle of tarsus	Same	Same
F. hal. brev. sesamoid	Absent	Absent	Absent	Absent	Present in 3 legs; absent in 4 legs	Present	Absent
Sesamoids in shank muscles	17 or 18	17 or 19	17 or 18	17 or 18	18	18	18
In shank	9	9	9	9	9	9	8
Short muscles of foot with sesamoids	1 or 2; Ext. hal. l. (Absent in 7 legs; a minute sesamoid present in 1 leg); Ext. brev. d. IV	2; Ext. hal. l.; Ext. brev. d. IV	1 or 2; Ext. hal. l. (Absent in 1 leg); Ext. brev. d. IV	1; Ext. brev. d. IV	2 or 3; Ext. hal. l.; Ext. brev. d. IV; F. hal. brev. (present in 3 legs, absent in 4 legs)	2 or 3; Ext. hal. l. (present in 1 leg); Ext. brev. d. IV; F. hal. brev.	1; Ext. brev. d. IV
Total	27 - 29	28 - 30	27 - 29	27 - 28	29 - 30	29 - 30	27

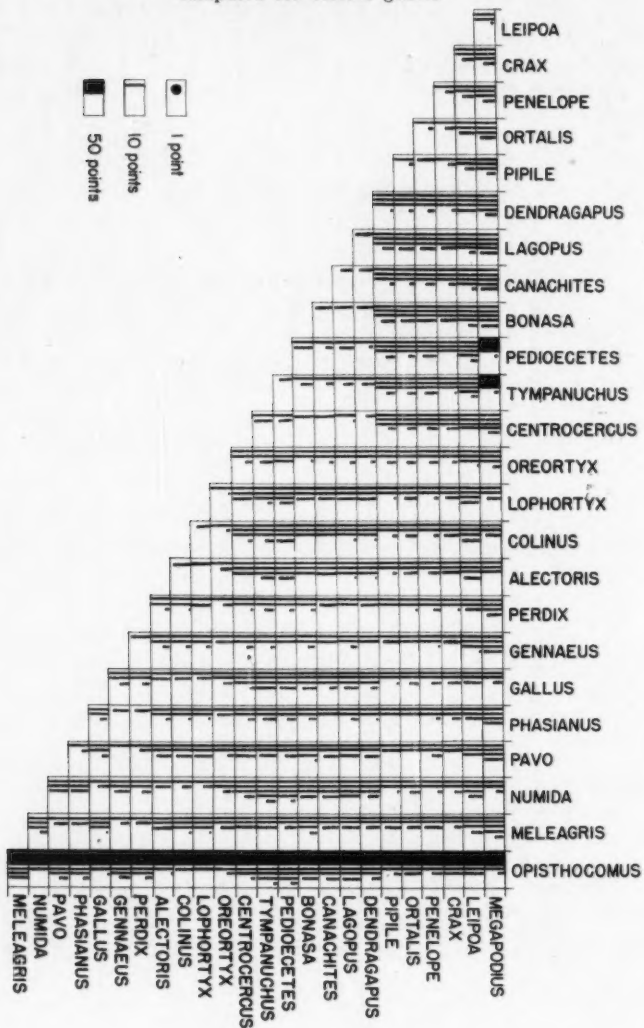
TABLE VII.—Principal differences noted within the family Phasianidae

	<i>Oreotyx</i>	<i>Lophortyx</i>	<i>Colinus</i>	<i>Alectoris</i>	<i>Perdix</i>	<i>Gallinarius</i>	<i>Gallus</i>	<i>Phasianus</i>	<i>Paro</i>
Ambiens belly	Short, ends about middle of femur	Short, ends about middle of femur or a little below	Ends a little below middle of femur	Ends far below middle of femur	Same	Same	Same	Same	Longest, ends about .3 femur
Fem. tib. ext. belly begins	About middle of femur	About middle	About middle	About middle	A little above middle of femur	Little above middle	Well above middle of femur	Well above middle	well above middle
Superficial tendons of Fem. tib. int.	Present on medial side	Present medial side	Present medial side	Present medial side	Present medial side	Present medial side	Superficial layer fleshy	Present	Superficial layer fleshy
P. caud. fem. of Piri.	Typical	Typical	Typical	Typical	Typical	Typical	Typical	Typical	No connection with tail
Belly of P. caud. fem. of Piri.	Broad	Broad	Broad	Broadest, almost as wide as P. il. fem., or less	Narrow, about $\frac{1}{2}$ width of P. il. fem., or less	Narrow, much less than $\frac{1}{2}$ width of P. il. fem.	Narrow, about $\frac{1}{2}$ width of P. il. fem., or less	Narrow, less than $\frac{1}{4}$ width of P. il. fem.	Extremely weak and narrow, about $\frac{1}{9}$ width of P. il. fem.
Belly of Tib. ant.	Ends far above loop	Ends distinctly above loop	Same	Same	Ends just above loop	Same	Extends to loop or a little above	Extends to loop or a little above	Extends to loop
Bifurcation of E. dig. I. tendon	About midway tarsus	Same	About midway tarsus or a little above	Well above tarsus	Same	About midway tarsus	About midway tarsus or below	A little above middle of tarsus	Will below middle of tarsus
Bony bridge in Gas. tendon in tarsus	Absent	Absent	Absent	Present in 1 leg; absent in 3 legs	Present	Present	Absent	Present	Present
Lateral head of Flex. per. d. III	Forms a separate tendon before uniting with medial head	Same	Same	Inserts fleshy on tendon of medial head	Forms a separate rate tendon above fusion	Forms a separate rate but short tendon above fusion	Inserts fleshy on tendon of medial head	Forms a separate rate but short tendon above fusion	Inserts fleshy rate but short on tendon of medial head
Abd. dig. II	Short, confined to much less than distal half of tarsus; medially situated, not extending onto anterior side of Tar. met.	Same	Same	Same	Same	Same (but about distal third of tarsus)	Long, usually extends above middle of tarsus; proximal end of belly on anterior side of Tar. met.	Short and medial, limited to about distal third of tarsus	Same
Add. d. II	Extends up to middle of tarsus or a little below	Extends to middle or a little above a little below	Extends up to middle or not nearly this high	Extends up to middle of tarsus or a little below	Extends up to middle of tarsus or a little below	Short, limited to about distal third of tarsus	Usually extends up to middle or a little above of 1 leg only.	Short, limited to about distal third of tarsus	Does not extend quite up to middle of tarsus
Sesamoids in Shank	15	0	0	0	17-19	18 or 19	0 or 1 (In Plan. of 1 leg only)	16-18	18
In Shank	6	3	3	3 or 4 (4 in 1 leg only)	10	9	8	10	9
Short muscles of foot with sesamoids	0	0	0	0	2 or 3	3	0	0-3	3
Total	21	3	3	3 or 4	29-32	30-31	8 or 9	27-31	30

TABLE VIII.—Some Muscle Measurements Used in Computing Quantitative Comparisons

	Ambiens belly ends	Fem. tib. ext. up to	Acc. semit. up to	Ext. dig. I. bifurcates on tarsus	Ext. hol. I. belly ends	Ext. pro. d. III belly begins	Ext. brev. d. IV belly ends	Abd. dig. II reaches up to	Add. d. II reaches up to	F. hol. brev. belly ends
Megapodius	.80	.28	.67	.85	.74	.41	.98	.16	.38	.69
Leipod	.89 (88-90)	.30 (28-32)	.59 (56-61)	.69 (67-71)	.76 (74-78)	.24 (23-25)	.85 (84-86)	.21 (19-24)	.47 (46-48)	.67 (64-71)
Crox	.68 (66-71)	.36 (34-39)	.51 (47-58)	.57 (55-58)	.80 (80-81)	.41 (39-43)	.85 (85-86)	.62 (61-62)	.52 (52-53)	.70 (70-72)
Penelope	.56 (52-59)	.49 (47-51)	.57 (53-62)	.60 (57-62)	.68 (79-92)	.51 (43-63)	.88 (85-90)	.59 (54-63)	.52 (45-59)	.65 (63-67)
Ortalis	.64 (62-66)	.47 (46-49)	.52 (44-57)	.48 (46-50)	.84 (81-88)	.53 (50-55)	.92 (88-98)	.68 (67-68)	.51 (47-55)	.71 (68-75)
Pipile	.63	.45	.56	.62	.78	.49	.86	.52	.54	.54
Dendragapus	.66 (51-72)	.52 (49-56)	.65 (58-68)	.51 (46-55)	.60 (48-67)	.58 (54-62)	.60 (51-78)	.58 (56-60)	absent	.58 (55-60)
Lagopus	.67 (62-73)	.55 (50-58)	.67 (62-73)	.66 (58-69)	.49 (41-71)	.62 (54-67)	.37 (32-47)	.60 (57-65)	absent	.43 (50-48)
Canachites	.62 (50-67)	.52 (50-53)	.66 (65-68)	.47 (45-51)	.70 (67-74)	.62 (60-65)	.47 (44-51)	.61 (54-68)	absent	.38 (35-42)
Bonasa	.63 (59-72)	.52 (49-54)	.69 (67-70)	.44 (38-48)	.59 (48-67)	.61 (47-72)	.43 (41-46)	.66 (65-67)	absent	.47 (41-53)
Pediocetes	.67 (62-70)	.51 (47-54)	.38 (34-42)	.52 (41-69)	.70 (67-73)	.62 (56-65)	.62 (56-76)	.61 (57-66)	absent	.57 (51-63)
Tympanuchus	.64 (62-66)	.52 (51-52)	.56 (55-58)	.56 (54-57)	.71 (69-74)	.67 (65-70)	.57 (57-57)	.59 (57-61)	absent	.60 (59-61)
Centrocercus	.57 (55-58)	.58 (56-60)	.63 (57-67)	.51 (48-54)	.44 (42-47)	.64 (61-67)	.59 (57-61)	.52 (50-55)	absent	.57 (50-63)
Oreortyx	.51 (48-53)	.51 (46-59)	.61 (57-64)	.58 (54-62)	.62 (48-72)	.66 (62-68)	.75 (71-80)	.59 (57-62)	.51 (45-59)	.64 (61-67)
Lophortyx	.58 (54-59)	.50 (47-54)	.58 (55-61)	.55 (53-57)	.66 (63-70)	.67 (66-68)	.85 (83-87)	.58 (53-60)	.46 (42-59)	.59 (57-63)
Colinus	.63 (59-69)	.51 (41-65)	.55 (46-62)	.48 (45-53)	.72 (66-76)	.65 (48-70)	.83 (76-90)	.58 (51-64)	.50 (42-63)	.69 (66-73)
Alectoris	.68 (60-75)	.53 (50-58)	.59 (50-66)	.41 (39-43)	.55 (44-67)	.75 (69-80)	.78 (74-80)	.66 (58-78)	.62 (52-69)	.65 (60-69)
Perdix	.73 (67-82)	.48 (44-52)	.60 (56-64)	.43 (40-48)	.73 (70-76)	.57 (51-62)	.72 (68-90)	.56 (53-60)	.54 (48-62)	.56 (49-60)
Gennaeus	.67 (66-68)	.49 (48-50)	.62 (62-62)	.50 (49-51)	.74 (74-74)	.56 (55-57)	.88 (87-88)	.71 (70-72)	.68 (67-68)	.49 (48-50)
Gallus	.71 (65-80)	.42 (36-47)	.56 (52-62)	.57 (47-67)	.72 (42-81)	.50 (41-58)	.84 (77-88)	.44 (36-56)	.46 (41-55)	.59 (56-70)
Phasianus	.69 (65-73)	.45 (43-48)	.56 (53-60)	.44 (33-52)	.65 (59-76)	.67 (61-72)	.85 (80-90)	.67 (64-68)	.64 (59-67)	.42 (35-52)
Pavo	.79 (77-80)	.45 (41-49)	.50 (45-54)	.60 (59-60)	.78 (77-78)	.54 (54-54)	.86 (86-88)	.69 (68-69)	.56 (55-57)	.70 (68-71)
Nimda	.76 (72-82)	.45 (44-48)	.47 (40-53)	.45 (43-48)	.73 (70-76)	.44 (42-48)	.85 (83-86)	.52 (49-50)	.48 (43-56)	.64 (60-67)
Melaeognis	.77 (72-83)	.41 (36-47)	.57 (54-60)	.50 (46-56)	.71 (64-75)	.56 (52-62)	.86 (85-87)	.67 (61-69)	.63 (58-70)	.59 (57-61)
Ophithocornus	.55 (48-61)	.57 (55-60)	.51 (43-57)	.95 (93-98)	.80 (76-85)	.09 (08-16)	.86 (80-90)	.37 (36-40)	.09 (07-11)	.77 (75-82)

TABLE IX.—Summary of arbitrary points of difference computed for various genera



QUANTITATIVE COMPARISON OF DIFFERENCES BETWEEN  
LEG MUSCLES OF VARIOUS GENERA AND FAMILIES

In an attempt to make quantitative comparisons of the differences in the leg muscles of various gallinaceous birds, we have followed the general scheme used for insects by Forbes (1934) and James (1953), with modifications. Muscles showing important modifications were graded on a system of 0-6 points to express the degree of difference between forms being compared. For each muscle considered in these comparisons arbitrary values were assigned objectively where the variation has been measured, and subjectively where the variation did not lend itself to direct measurement. In a few cases where the structure was not consistent within a species, interpolation was necessary.

In arriving at a figure expressing the difference between any two forms involving a muscle character subject to measurement, the mean condition in one form for any given characteristic was compared with the mean in another. For example, in comparing the length of the Abd. dig. II in *Canachites* and *Opisthocomus*, according to our measurements (Table VIII), this muscle began at .36 to .40 tarsometatarsus with a mean of .37 in *Canachites*, and .54 to .68 tarsometatarsus with a mean of .61 in *Opisthocomus*. To get the points of difference between these two we subtracted .37 from .61, giving a difference of .24. Using the formula  $M_1 - M_2 \times 5 = X$  we obtained a value of 1.2 points of difference on our arbitrary scale of 0-6. We felt that a difference of this kind and magnitude did not justify a higher value. All comparisons based on measurements were treated in this manner. The figures obtained by comparing one genus with another in regard to the following characteristics were totaled and adjusted to the nearest whole number to give the points of difference shown on Table IX.

Il. troc. med.—Scored 0 or 3 points, based on whether or not this muscle is separate or fused with the Il. troc. ant.

Glut. med. et min.—0, 1 or 2 points for differences in relative size and extent of origin.

Ambiens—Width of belly: 0, .5 or 1 point. Length of belly: 0-1.9 points based on measurements. Tendon: 3 points between the normal condition and the disappearance of this structure at the knee as in *Opisthocomus*.

Fem. tib.—Extent of origin of Fem. tib. ext.: 0-1.5 points based on measurements. Fem. tib. int.: 0 or 1 point based on whether or not the superficial layer at the distal end is fleshy or tendinous.

Piriformis.—Presence or absence of P. caud. fem.: 0 or 6 points. Origin of P. caud. fem. by a definite tendon or not: 0, 1 or 2 points. Relative width of P. caud. fem. belly: 0, 1 or 2 points. Origin of P. caud. fem. normal or without any connection to tail as in *Pavo*: 0 or 3 points. Fusion of P. caud. fem. with P. il. fem. typical or posteriorly situated as in *Crax*: 0 or 1 point. Tendinous area on dorsal edge of P. il. fem. present or absent: 0 or 1 point.

Semitendinosus.—Usual condition or no connection with caudal

vertebrae as in *Opisthocomus*: 0 or 2 points. Pelvic origin typical or extending onto ischium as in *Ortalis*: 0 or 1 point. Extent of insertion of accessorius on posterior side of femur: 0-1.6 points based on measurements.

Semimembranosus.—Belly weak to strong: 0, 1 or 2 points. Position of origin anteriorly to posteriorly situated: 0-2 points. Typical condition, or origin not connected with pubis as in *Opisthocomus*: 0, or 1 point.

Isch. fem.—Posterior end of belly extends to posterior edge of ischium or not: 0, 1 or 2 points.

Obt. int.—Portion of the origin from ventrolateral surface of ilium absent, small, or large: 0, 1, 2 or 3 points.

Add. long.—Relative size of P. ext. compared to P. int.: 0-3.5 points. Insertion of P. int. tendinous or fleshy: 0 or 1 point.

Tib. ant.—Belly short to long: 0, 1 or 2 points.

Ext. dig. I.—Belly typical or broad as in *Opisthocomus*: 0 or 1 point. Division of tendon in tarsal region proximal to distal: 0-2.7 points based on measurements. Insertion typical or with a single tendon to each foretoe as in *Opisthocomus*: 0 or 1 point.

Per. long.—Typical or greatly modified as in *Opisthocomus*: 0 or 4 points.

Gastrocnemius.—P. int. extending around knee or not: 0 or 2 points. Tendon single to double: 0, 1 or 2 points.

F. p. et p. d. II.—Belly typical or short as in *Opisthocomus*: 0 or 2 points. Belly single or with two heads: 0 or 1 point.

Vinculum between Flex. per. d. III and F. p. et p. d. III.—Present or absent: 0 or 5 points.

Flex. per. d. II.—Typical or lateral head unusually large as in *Opisthocomus*: 0 or 2 points.

Flex. per. d. III.—Lateral head with no tendon, short, or long tendon: 0, 1 or 2 points.

F. hal. I.—Belly typical or long: 0 or 2 points. Proximal end of tendon typical or broad and flat as in *Numida*: 0 or 1 point.

Ext. hal. I.—Length of belly: 0-2.1 points based on measurements.

Ext. pro. d. III.—Relative length of muscle: 0-3.2 points based on measurements.

Ext. brev. d. IV.—Relative length of tendon: 0-3.1 points based on measurements. Typical or muscle beginning farther distally as in *Opisthocomus*: 0 or 1 point.

Abd. dig. II.—Relative length of muscle: 0-2.8 points based on measurements. Belly typical or extending onto anterior side of tarsus: 0 or 2 points. Insertion typical or posteriorly situated as in *Opisthocomus*: 0 or 1 point.

F. hal. brev.—Belly short to long: 0-1.9 points based on measurements. Belly typical or ensheathing F. dig. I. tendon: 0 or 1 point. Tendon typical or divided distally as in Megapodiidae: 0 or 2 points.

Add. d. II.—Present or absent: 0 or 6 points. Relative length of



muscle: 0-2.9 points based on measurements. Tendon typical or long as in *Opisthocomus*: 0 or 1 point.

Lumbricalis.—Typical or two-headed and large as in *Opisthocomus*: 0 or 3 points.

Shank muscle sesamoids.—Quantitative expression as follows:

Difference in number in shank	Points allotted
1 - 2	1
3 - 4	2
5 - 6	3
7 - 11	4
12 - 14	5
15 - 19	6
Difference in number in tarsus	Points allotted
1	1
2 - 3	2
4 - 5	3
6 - 7	4
8 - 9	5

Short foot muscle sesamoids.—Quantitative expression as follows:

Difference in number present	Points allotted
1	1
2	2
3	3
4	4

TABLE X.—Summary of points of difference between and among the various taxonomic groups

	Megapodiidae	Cracidae	Tetraonidae	Phasianidae	Numida	Meleagris	Opisthocomus
Megapodiidae	21.2	24.4-37.1 M.30.3	39.0-52.1 M.44.9	24.2-38.9 M.31.9	22.9-35.6 M.29.2	34.6-43.8 M.39.2	62.9-69.4 M.66.2
Cracidae		7.8-14.4 M.12.2	30.0-38.8 M.34.1	18.2-29.1 M.22.7	20.9-24.3 M.22.5	22.9-27.9 M.25.9	62.6-70.4 M.66.4
Tetraonidae			4.4-18.4 M.10.8	18.1-39.9 M.27.3	34.8-44.5 M.38.8	25.1-32.7 M.28.2	72.5-82.7 M.77.6
Phasianidae				6.0-28.2 M.17.8	14.3-29.0 M.21.6	14.5-31.4 M.23.6	58.1-74.6 M.66.5
Numida						33.0	59.9
Meleagris							79.8

In comparing the twenty-five genera studied in regard to the foregoing twenty-nine sets of characteristics we made up tables totaling 8700 entries, which are, unfortunately, too voluminous to reproduce here.

SYNOPSIS OF THE PRINCIPAL MYOLOGICAL CHARACTERS OF THE  
PELVIC LIMB OF THE SUBORDER GALLI

*Myological Formula.*—ABCDXYAmV in all except *Meleagris* which lacks A.

*Muscles Absent.*—*Pars caudifemoralis* of the *piriformis* in *Meleagris*; Adductor digiti II in the Tetraonidae.

*Rudimentary.*—Lumbricalis.

*Deep Flexor Tendons.*—Connected by a vinculum which varies greatly in extent. Type I (Gadow, 1891:195).

*Perforation of Hypotarsus by Flexor Tendons.*—Sometimes two closed bony canals, usually only one — that enclosing the F. dig. I. In a few cases the bony groove enclosing the tendons of the Flex. per. d. II and F. p. et p. d. II is roofed over with bone. The F. hal. I. traverses an open bony groove on the lateral side.

*Other Important Modifications.*—Fem. tib. ext. independently developed; origin of semitendinosus includes proximal caudal vertebrae; origin of Obt. int. from ventrolateral surface of ilium always present, but varies greatly in extent in the different groups; Add. long. consists of a P. ext. and P. int.; no definite accessory tendon of insertion to the Tib. ant.; tendon of Ext. dig. I. generally bifurcates near the middle of the tarsometatarsus except in *Lagopus*, which divides near the distal end; belly of Per. long. broad, enveloping most of the Tib. ant. and extending up to knee; P. int. M. gas. extends around the front of the knee; tendon of the gastrocnemius single in some forms, but in others there are two separate tendons that unite above the Tib. cart.; origin of F. p. et p. d. III not connected with fibular shaft; lateral head of Flex. per. d. II very small; Flex. per. d. III with two heads, the lateral without a separate tendon in some forms; Flex. per. d. IV with a small head lateral to the biceps tendon; F. hal. I. with a single head; tendon of F. hal. I. perforates that of the F. hal. brev.; Ext. hal. I. with a short distal head in some forms, but not in others; Ext. pro. d. III short in most forms but long in others; Abd. dig. II limited to about distal third to half of tarsus in most forms, but considerably longer in Megapodiidae and *Gallus*; tendon of F. hal. brev. single in most forms but divided in *Megapodius* and *Leipoa*; supernumerary sesamoids in the pelvic limb: most forms have between 17 and 30, but in a few the number is reduced to two or three.

SYNOPSIS OF THE PRINCIPAL MYOLOGICAL CHARACTERS OF THE  
PELVIC LIMB OF THE SUBORDER OPISTHOCOMI

*Myological Formula.*—ABDXYAim.

*Muscles Absent.*—None.

*Rudimentary*.—None.

*Deep Flexor Tendons*.—Connected by a simple vinculum. Type I (Gadow, 1891:195).

*Perforation of Hypotarsus by Flexor Tendons*.—Only the F. dig. I. passes through a closed bony canal. The Flex. per. d. II and F. p. et p. d. II pass through a groove which is not roofed over with bone, and the F. hal. I. passes through a similar groove on the lateral side.

*Other Important Modifications*.—Il. troc. med. fused with Il. troc. ant.; tendon of ambiens disappears at knee without reaching the lateral heads of the flexor perforatus muscles; Fem. tib. ext. independently developed but short; origin of semitendinosus not connected with caudal vertebrae; Obt. int. not connected with ventrolateral surface of ilium; Add. long. consists of a P. ext. and a P. int.; Tib. ant. without definite accessory tendon of insertion; tendon of Ext. dig. I. trifurcates near distal end of tarsus, sending an undivided branch to each fore toe; belly of Per. long. short, limited to about the distal two-thirds of shank and situated entirely on the lateral side without enclosing Tib. ant.; P. int. M. gas. does not extend around the front of knee; Gas. tendon single; origin of F. p. et p. d. III not connected with fibular shaft; vinculum between Flex. per. d. III and F. p. et p. d. III absent; lateral head of Flex. per. d. II larger than medial head; lateral head of Flex. per. d. III with separate tendon; Flex. per. d. IV with a small head lateral to the biceps tendon; F. hal. I. with a single head; tendon of F. hal. I. perforates that of F. hal. brev.; Ext. hal. I. with a distinct distal head; Ext. pro. d. III long, extending above Tib. ant. insertion; Abd. dig. II extends above middle of tarsus, the insertion very peculiar, mainly on the posterior surface of Phal. I; F. hal. brev. powerfully developed, the tendon single; Add. d. II very long, reaching hypotarsus, the tendon long; lumbricalis very strongly developed, with two long, distinct bellies; supernumerary sesamoids in the pelvic limb: only one, in the tendon of the F. dig. I. in the tarsus.

#### DISCUSSION AND CONCLUSIONS

The following remarks can be only tentative in view of the small number of forms available for study, especially in some groups. We would like to make it clear at this point that our descriptions concern only specimens listed under "Material and Methods" and it must be left to future studies to determine to what extent these observations apply throughout the various families and genera.

The Megapodiidae and Cracidae are generally considered to be the most primitive of gallinaceous birds and a study of the muscles of the pelvic limb seems to corroborate this, since there are few unusual modifications. Among the apparently primitive characteristics are the long bellies with relatively short tendons of the shank and foot muscles compared with those in some of the more specialized groups of the order. The more important functional development of the hallux is clearly indicated by the strong foot muscles supplying this digit. The

short head of the Ext. hal. I. is unusually distinct in the Megapodiidae and Cracidae in contrast to the other forms except *Opisthocomus* — perhaps another primitive condition. A specialization of these two families is seen in the belly of the F. hal. brev. which ensheathes the tendon of the F. dig. I. near the base of the tarsus, a condition not found in any of the other groups. Our representatives of these two families show some important differences: the position of the origin of the semimembranosus is about midway the ischium in the Cracidae, but is in the typical, more posterior, position in the Megapodiidae; the belly of the F. hal. I. in the Megapodiidae is considerably longer and stronger than in the Cracidae or in any of the other groups of this order except *Opisthocomus*; the tendon of the F. hal. brev. is divided shortly before its insertion in our representatives of the Megapodiidae but not in other forms (Gadow, 1891:202, reported a similar condition in *Talegalla*). The score of 30.3 points of difference between the Megapodiidae and Cracidae on our arbitrary scale (Table X) is based, to a considerable extent, on a comparison of the number of supernumerary sesamoids. This difference is probably much higher than it would have been if we had used an adult specimen of *Megapodius*. The presence of a short sesamoid in the peroneus longus of this specimen suggests very strongly that it was taken at a stage when the sesamoids were just beginning to develop. Our observations tend to confirm the validity of the Superfamily Cracoidea (Peters, 1934:3).

In the Family Megapodiidae our material was too sparse to justify any conclusions as to differentiation within the group, although certain minor differences were noted between *Megapodius* and *Leipoa* (Table IV). Over half of the 21.2 points of difference for these two forms (Table X) are based on the very small number of sesamoids in our immature specimen of *Megapodius*.

In the Family Cracidae the leg myology does not suggest any subdivisions, but certain characteristics are worth noting. The piriformis differs in *Crax* in that the fusion of the P. caud. fem. with the P. il. fem. occurs about one inch posterior to the femur, much farther back than in other forms; in *Pipile* the sesamoid of the E. dig. I. in the foot does not have the medial branch ossified as in the other three genera studied. The peroneus longus sesamoid in the shank is present in *Crax* and *Ortalis*, but absent in *Penelope* and *Pipile*. The plantaris sesamoid was found only in *Ortalis*. In *Penelope* the two heads of the Flex. per. d. III form separate tendons but there is only one tendon in the other three genera. A sesamoid was found in the tendon of the Ext. hal. I. only in *Penelope*, although it was absent in one leg of this form. *Penelope* and *Pipile* show the greatest similarity among the four genera studied (Table IX).

The Family Tetraonidae shows only one peculiar condition, the uniform absence of the Add. d. II, there being no indication of this muscle in any of the specimens examined. In addition there is a tendency for the short muscles of the foot to be weak and attenuated,

with relatively short bellies. This might be considered an adaptation to extreme cold since many of these birds are found in high latitudes, particularly *Lagopus*, in which this condition is best illustrated. As suggested in Table X the Tetraonidae, compared with the more primitive Megapodiidae and Cracidae, appear to be rather highly specialized and more closely related to the Phasianidae than to any other group.

Within the Family Tetraonidae there is considerable uniformity in the muscles of the pelvic limb; however, some trends may be noted (Tables VI, IX). *Pedioecetes* and *Tympanuchus* agree in the following conditions which differ from the other forms studied: the short ischiofemoralis leaves a wide area of ischium exposed; the very large P. int. of the Add. long. is several times as large as the P. ext., and the P. ext. of this muscle is very short, ending about midway the thigh or above; a sesamoid was found in the tendon of the F. hal. brev. *Pedioecetes* differs from *Tympanuchus* in having the belly of the semitendinosus very broad and the accessorius insertion extending far above the middle of the femur; *Tympanuchus* is more typical in that the belly of this muscle is narrower and the accessorius does not extend up to the middle of the femur. The tendon of the F. dig. I. in the hypotarsus is enclosed in a bony canal in *Pedioecetes* but runs through an open groove in our specimen of *Tympanuchus*. Relatively little variation was found in the five other genera of Tetraonidae but several points are worth noting. *Dendragapus* and *Canachites* appear to be quite conservative and show no unusual modifications; the only difference of importance between the two is in the belly of the Ext. hal. I. which is attenuated near the middle of the tarsus in *Canachites* but not in *Dendragapus*. *Lagopus* is peculiar in having the division of the tendon of the Ext. dig. I. far down, opposite Met. I, rather than near the middle of the tarsus as in the other genera. The belly of the Ext. hal. I. is reduced in *Lagopus* but this is not the case in *Bonasa* which shows no unusual condition. *Centrocercus* differs from other Tetraonidae as follows: The belly of the ambiens is short and does not extend down to the middle of the thigh; the bony bridge in the gastrocnemius tendon in the region of the tarsus is absent; the belly of the Ext. hal. I. is short, ending about midway the tarsus. The absence of a sesamoid in the Ext. hal. I. was noted consistently only in *Bonasa* and *Centrocercus*.

The Phasianidae as a whole shows no peculiar condition in the leg musculature. Since the Add. d. II is well developed in these birds they are more primitive in this respect than the Tetraonidae in which this muscle is absent. The Phasianidae shows the greatest intra-family differentiation (Tables VII, IX, X). One of the most striking observations in regard to this group involves the similarity in sesamoids between the New World quails *Callipepla*, *Colinus*, *Odontophorus*, and *Lophortyx*, and the Old World partridge *Alectoris*. They not only have the number greatly reduced, but the same three are consistently present, although *Odontophorus* and *Alectoris* may have a

fourth (Table III). *Oreortyx*, on the other hand, although otherwise fairly similar to other American quails studied, has 21 supernumerary sesamoids in the pelvic limb. It seems unlikely that this amazing similarity between *Callipepla*, *Colinus*, *Otontophorus*, *Lophortyx*, and *Melotris* could be due to convergence. This throws considerable doubt on the validity of the Subfamily Otontophorinae and makes the examination of additional genera highly desirable. On our scale of comparison *Pedix*, *Gallinago*, *Phasianus* and *Bonasa* differ by only seven to 15 points, the greatest disparity being shown by *Bonasa* with its greatly reduced and highly modified P. caud. fem. of the Ptil. *Gallus* (1891:159) and Ridgway and Freedmann (1946:2) indicated that the P. caud. fem. is absent in this genus. The absence of sesamoids in the skull of the domestic fowl is apparently an original condition of these birds since we found the same in a specimen of the jungle fowl, *Gallus gallus*. So far as known *Gallus* is the only gallinaeous bird that normally has no sesamoids in the skull but almost a full complement in the tarsus (Table II).

There is nothing unusual in the musculature of *Vormide* except the great reduction in the number of ossified tendons, only two being present, in the F. dig. II and F. hal. II in the region of the tarsus (Tables II, III). There is nothing in the present study to suggest that *Vormide* should be considered anything more than a member of the Family Phasianidae, perhaps in a separate subfamily as suggested by Delacour (1951:23) and May and Amadon (1951:35).

As previously reported by Gudow (1891:159), *Melospiza* is peculiar in lacking the P. caud. fem. of the pterocera. The only other peculiarity we noted in this bird is the occasional presence of a vinculum between the tendons of the Flex. per. d. II and the F. p. e. p. d. II just above the base of the toe toe. This was found in four out of thirty-nine specimens; bilaterally in only one. Mitchell (1901:533) reported such a connection in *Baleornis*, and Kopper (1926:201) in *Megala*. Fisher and Goodman (1955:94) reported a "fusion" of these tendons in *Grus canadensis*. Hudson (1937) did not find such a structure in this species. Apparently the vinculum between the Flex. per. d. II and F. p. e. p. d. II is rare and of irregular occurrence in birds; however, the fact that it occurs at all indicates that ancession or nodus birds might have had this structure as a constant feature of their anatomy, especially in view of the fact that it has been reported in three modern orders. The similarity of this vinculum to the one associated with the perforated flexors to the third toe in many birds suggests a primitive condition. The musculature of the pelvic limb in *Melospiza* suggests that it is a typical pheasant that has lost the P. caud. fem. of the Ptil. (Table IX).

*Opisthocoma* (Tables III, IX) is so different from the more typical gallinaeous birds in so many ways that it should be placed either in a separate order or at least in a different suborder—Opisthocomi; the latter was done by Peters (1934:14) and Ridgway and Freedmann (1946:4). *Opisthocoma* is unique among all gallinaeous birds



examined in the following respects: the Il. troc. med. is completely fused with the Il. troc. ant.; the ambiens tendon usually disappears in the knee region; the semitendinosus arises from the ilium only and has no connection with caudal vertebrae; the origin of the Obt. int. has no connection with the ventrolateral surface of the ilium; the tendon of the Ext. dig. I. trifurcates near the end of the tarsus, sending a single branch to each fore toe; the Per. long. is short, narrow and lateral, in striking contrast to the condition in other types; the P. int. of the gastrocnemius does not extend around the front of the knee; the belly of the F. p. et p. d. II is very short; the vinculum between the tendons of the Flex. per. d. III and F. p. et p. d. III is absent; the main head of the Flex. per. d. II is lateral rather than medial to the tendon of the biceps femoris; the insertion of the Abd. dig. II is mainly on the posterior rather than the lateral side of the base of the proximal phalanx; the lumbricalis consists of two long bellies instead of one feeble belly; there is only one supernumerary sesamoid in the pelvic limb, this being in the tendon of the F. dig. I. in the region of the tarsus.

The vinculum between the tendons of the F. dig. I. and F. hal. I. in the region of the tarsus represents Gadow's Type 1 (1891:195). It varies greatly in extent among the different genera of gallinaceous birds but the variations appear to have no taxonomic significance. The vinculum between the tendons of the Flex. per. d. III and F. p. et p. d. III just above the bases of the toes, is well developed in all specimens except *Opisthocomus* in which no trace could be found. The fact that this vinculum is well developed in all of the typical galliform birds indicates that this is a primitive characteristic. This group appears to be far more conservative in this regard than *Grus* as described by Fisher and Goodman (1955:97), since they indicate that it was present in *Grus canadensis* but absent in *Grus americana*. Variation of this type in regard to the vinculum in question must be very unusual in birds since we have encountered no similar case either in the Order Galliformes or elsewhere.

In regard to the Il. troc. med. in birds generally, it is clear that this muscle is separate from the other two Il. troc. muscles in many groups but is fused with the Il. troc. ant. in others. In those forms in which the muscle is not separate, the position of nerves perforating the belly of the combined Il. troc. med. plus Il. troc. ant. make it obvious that the Il. troc. med. is represented but is simply fused with the Il. troc. ant. In forms in which the Il. troc. med. is a separate muscle the same nerves extend between the two.

Without a thorough study of the locomotor habits of living examples of the various genera it is impossible to reach an understanding of the significance of differences in the structure and proportions of the various muscles. However, it might be of interest to comment briefly on a few of the more obvious possibilities. Perhaps it is significant that the P. caud. fem. of the piriformis is absent in *Meleagris* and does not connect with the tail in *Pavo*: the two genera are known



fourth (Table II). *Oreortyx*, on the other hand, although otherwise fairly similar to other American quails studied, has 21 supernumerary sesamoids in the pelvic limb. It seems unlikely that this amazing similarity between *Callipepla*, *Colinus*, *Odontophorus*, *Lophortyx*, and *Alectoris* could be due to convergence. This throws considerable doubt on the validity of the Subfamily Odontophorinae and makes the examination of additional genera highly desirable. On our scale of comparison *Perdix*, *Gennaeus*, *Phasianus* and *Pavo* differ by only seven to 15 points, the greatest disparity being shown by *Pavo* with its greatly reduced and highly modified P. caud. fem. of the Pirif. Gadow (1891:159) and Ridgway and Friedmann (1946:2) indicated that the P. caud. fem. is absent in this genus. The absence of sesamoids in the shank of the domestic fowl is apparently an original condition of these birds since we found the same in a specimen of the jungle fowl, *Gallus gallus*. So far as known *Gallus* is the only gallinaceous bird that normally has no sesamoids in the shank but almost a full complement in the tarsus (Table II).

There is nothing unusual in the leg musculature of *Numida* except the great reduction in the number of ossified tendons, only two being present, in the F. dig. I. and F. hal. I. in the region of the tarsus (Tables II, III). There is nothing in the present study to suggest that *Numida* should be considered anything more than a member of the Family Phasianidae, perhaps in a separate subfamily as suggested by Delacour (1951:23) and Mayr and Amadon (1951:33<sup>4</sup>).

As previously reported by Gadow (1891:159), *Meleagris* is peculiar in lacking the P. caud. fem. of the piriformis. The only other peculiarity we noted in this bird is the occasional presence of a vinculum between the tendons of the Flex. per. d. II and the F. p. et p. d. II just above the bases of the fore toes. This was found in four out of thirty-nine specimens; bilateral in only one. Mitchell (1901:653) reported such a connection in *Balearica*, and Kopperi (1928:201) in *Mergus*. Fisher and Goodman (1955:94) reported a "fusion" of these tendons in *Grus canadensis*; Hudson (1937) did not find such a structure in this species. Apparently the vinculum between the Flex. per. d. II and F. p. et p. d. II is rare and of irregular occurrence in birds; however, the fact that it occurs at all indicates that ancestors of modern birds might have had this structure as a constant feature of their anatomy, especially in view of the fact that it has been reported in three modern orders. The similarity of this vinculum to the one associated with the perforated flexors to the third toe in many birds suggests a primitive condition. The musculature of the pelvic limb in *Meleagris* suggests that it is a typical pheasant that has lost the P. caud. fem. of the Pirif. (Table X).

*Opisthocomus* (Tables III, IX) is so different from the more typical gallinaceous birds in so many ways that it should be placed either in a separate order or at least in a different suborder—Opisthocomi; the latter was done by Peters (1934:141) and Ridgway and Friedmann (1946:4). *Opisthocomus* is unique among all gallinaceous birds

examined in the following respects: the Il. troc. med. is completely fused with the Il. troc. ant.; the ambiens tendon usually disappears in the knee region; the semitendinosus arises from the ilium only and has no connection with caudal vertebrae; the origin of the Obt. int. has no connection with the ventrolateral surface of the ilium; the tendon of the Ext. dig. I. trifurcates near the end of the tarsus, sending a single branch to each fore toe; the Per. long. is short, narrow and lateral, in striking contrast to the condition in other types; the P. int. of the gastrocnemius does not extend around the front of the knee; the belly of the F. p. et p. d. II is very short; the vinculum between the tendons of the Flex. per. d. III and F. p. et p. d. III is absent; the main head of the Flex. per. d. II is lateral rather than medial to the tendon of the biceps femoris; the insertion of the Abd. dig. II is mainly on the posterior rather than the lateral side of the base of the proximal phalanx; the lumbricalis consists of two long bellies instead of one feeble belly; there is only one supernumerary sesamoid in the pelvic limb, this being in the tendon of the F. dig. I. in the region of the tarsus.

The vinculum between the tendons of the F. dig. I. and F. hal. I. in the region of the tarsus represents Gadow's Type 1 (1891:195). It varies greatly in extent among the different genera of gallinaceous birds but the variations appear to have no taxonomic significance. The vinculum between the tendons of the Flex. per. d. III and F. p. et p. d. III just above the bases of the toes, is well developed in all specimens except *Opisthocomus* in which no trace could be found. The fact that this vinculum is well developed in all of the typical galliform birds indicates that this is a primitive characteristic. This group appears to be far more conservative in this regard than *Grus* as described by Fisher and Goodman (1955:97), since they indicate that it was present in *Grus canadensis* but absent in *Grus americana*. Variation of this type in regard to the vinculum in question must be very unusual in birds since we have encountered no similar case either in the Order Galliformes or elsewhere.

In regard to the Il. troc. med. in birds generally, it is clear that this muscle is separate from the other two Il. troc. muscles in many groups but is fused with the Il. troc. ant. in others. In those forms in which the muscle is not separate, the position of nerves perforating the belly of the combined Il. troc. med. plus Il. troc. ant. make it obvious that the Il. troc. med. is represented but is simply fused with the Il. troc. ant. In forms in which the Il. troc. med. is a separate muscle the same nerves extend between the two.

Without a thorough study of the locomotor habits of living examples of the various genera it is impossible to reach an understanding of the significance of differences in the structure and proportions of the various muscles. However, it might be of interest to comment briefly on a few of the more obvious possibilities. Perhaps it is significant that the P. caud. fem. of the piriformis is absent in *Meleagris* and does not connect with the tail in *Pavo*; the two genera are known

to elevate the tail a full 90 degrees or more in strutting; such extreme elevation of the tail might place too much stress on the muscle in question, if it connected the femur and tail as in most birds. As pointed out by Gadow (1891:148) the ambiens is usually absent in climbing birds such as parrots; lack of a connection in *Opisthocomus* between this muscle and the perforated flexors might be correlated with arboreal habits. In the typical development of the ambiens the tendon exerts a slight pull on these flexors whenever the knee is bent, thereby possibly limiting to some degree the ability to extend the toes when reaching for a new hold, especially at a higher level. To check this point we manipulated the legs of living and freshly killed chickens and found that, although the bending of the knee causes the ambiens tendon to exert a pull on the perforated flexors, the force involved is very slight and is not sufficient to be transmitted to the toes. The lack of a connection between the powerful semitendinosus and the tail in *Opisthocomus* appears to permit the tail to engage in counterbalancing movements independent of leg action; this might be of some advantage in climbing. If *Opisthocomus* is to be considered a gallinaceous bird, the vinculum between the Flex. per. d. III and F. p. et p. d. III must have been lost independently of the loss of this structure in other groups of birds such as the Passeriformes; as an adaptation for climbing this might allow more independent action of these two muscles thus permitting perhaps more subtle bendings of the various segments of the third toe. Other peculiarities of *Opisthocomus* that appear to contribute to arboreal locomotion are the long, powerful belly of the F. hal. l., the larger and more powerful development of the short toe muscles, and the peculiar insertion of the Abd. dig. II which is mainly on the posterior side of Phal. I, Dig. II, causing this muscle to function as a flexor as well as abductor.

On the basis of our study of the muscles of the pelvic limb we agree with Sharpe (1891:70) and Beebe (1909:46) in removing *Opisthocomus* from the Order Galliformes and placing it in the Order Opisthocomiformes. Mayr and Amadon (1951:33) have recently proposed a classification of the Galli which includes the Subfamilies Phasianinae, Numidinae and Tetraoninae in the Family Phasianidae. We agree that the Subfamily Odontophorinae should be eliminated, placing the pheasants, quails, etc., in the Subfamily Phasianinae, and that the Numidinae should be designated a subfamily of the Phasianidae. However, we feel that the grouse should be kept in a separate family. Although it seems clear that they are closely related to the pheasants, nevertheless, they differ in certain important respects, for example, the feathered tarsi and the absence of the Adductor digiti II muscle.

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Studies on the Trematode Family Brachycoeliidae, II.  
Revision of the Genera *Glyphelmins* (Stafford,  
1900) Stafford, 1905, and *Margeana* Cort, 1919;  
and the Description of *Reynoldstrema* n.  
gen. (*Glyphelminae* n. subfam.)

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This paper represents the second of a monographic series on the trematode family Brachycoeliidae Johnston, 1912. In Part I (Cheng, 1957) the author referred to this family of flukes as members of the subfamily Brachycoeliinae Looss, 1899; however, at that time he stated that he agreed with Fuhrmann (1928) "... in retaining Brachycoeliinae as a subfamily under Dicrocoeliidae until additional evidences can indicate differently." Since the appearance of Part I, the life history of *Brachycoelium obesum* Nicoll, 1914 has been satisfactorily established and that of *B. salamandrae* (Frölich, 1789) has been partially established. The information obtained from these life cycles strongly suggest that the subfamily Brachycoeliinae should be granted independent status as the family Brachycoeliidae as suggested by Johnston (1912), since the life histories of the *Brachycoelium* spp. indicate the presence of only one intermediate host (the entire life histories will be published at a later date) which differs sharply from the life cycles of either the Dicrocoeliidae or the Plagiorchiidae where two intermediate hosts exist. Since Rankin's (1944) description of the life cycle of *Glyphelmins quieta* contained only one intermediate host, this further suggests the close relationship between *Glyphelmins* and *Brachycoelium*, hence the author has chosen to assign the genera covered in Part I and those included in Part II as members of the independent family Brachycoeliidae.

Inasmuch as the members of the genus *Brachycoelium* are different from those of *Glyphelmins* and *Margeana* (see Cheng, 1957) the author has chosen to retain the subfamily Brachycoeliinae Looss, 1899 under Brachycoeliidae to include *Brachycoelium* and has erected the *Glyphelminae* n. subfam., also under Brachycoeliidae, to include *Glyphelmins*, *Margeana* and *Reynoldstrema*.

This present paper consists of a revision of *Glyphelmins* (Stafford, 1900) Stafford, 1905, the re-establishment of *Margeana* Cort, 1919 as a valid genus, and the description of *Reynoldstrema* n. gen. The descriptions of the various species of the genera considered, have been restricted to the essentials for the sake of brevity. The original type drawings have been included to aid in the diagnosis of specimens.

The genera *Glyphelmins* and *Margeana* are extremely closely

related and their synonymy has been the subject of much postulation (Miller, 1930; Rankin, 1944; Babero, 1951; and others). Having reviewed the original generic diagnosis of *Glypthelmins* by Stafford (1905), the author agrees with Miller (1930) and Barbero (1951) in saying that much of the present confusion is due to the poor original generic characteristics established by Stafford. Miller (1930) redescribed the generotype, *G. quieta* (Stafford, 1900) Stafford, 1905, and in the same paper he transferred *Margeana californiensis* Cort, 1919 into this genus. However, he remarked that some of the described species of *Glypthelmins* did not satisfy the original descriptions for the genus inasmuch as they did not possess peripharyngeal glands which are distinctly present in *G. quieta*. Miller suggested revising the generic characteristics while Babero (1951) suggested the creation of another genus to include the species without peripharyngeal glands.

Barbero also noted that some species possessed pretesticular uterine coils while others did not, and suggested that a third genus might be erected to solve this difficulty. Having reviewed all the original descriptions and studied all available North American type specimens in addition to paratypes and specimens collected by the author, it is felt that the difference of pre- and post-testicular uterine coils is not of sufficient value to warrant differentiation on the generic level. Finally, since *Margeana californiensis*, the generotype, was described as a new genus because of the absence of peripharyngeal glands, the erection of another genus as suggested by Babero, is not necessary. The author is hereby proposing the re-establishment of *Margeana* as a valid genus.

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#### SUBFAMILY *Glypthelminae*, n. subfam.

##### Genus *GLYPTHELMINS* Stafford, 1905

The exact systematic position of *Glypthelmins* has been in debate as to whether it is a member of Brachycoeliinae (Dicrocoeliidae) or Plagiorchiniinae (Plagiorchidae). Olsen (1937), following the taxonomic pattern of Travassos (1926 a, b, c, d), Lucker (1931) and Mehra (1931 a, b), considers it to be a member of Plagiorchiniinae (syns. Lepodermatinae Looss, 1899; Haplometrinae Pratt, 1902; and Astiotrematinae Baer, 1924), while more recently, Byrd (1937) and Parker (1941) consider it a member of Brachycoeliinae. Undoubtedly, *Glypthelmins* closely resembles members of both subfamilies. The life-history of *G. quieta* as described by Rankin (1944)



duplicates the pattern of larval stages of the members of both Plagiorchiidae and Dicrocoeliidae; Plagiorchiidae, represented by *Plagitura salamandra* Holl, 1928, as described by Owen (1946), and Dicrocoeliidae, by *Conspicuum icteridorum* Denton and Byrd, 1951, as described by Patten (1952). Hence the life-cycle patterns contribute little information to the systematic position of *Glypthelmins*. Because of the intimately close host association of *Glypthelmins* and *Brachycoelium*, both parasitizing amphibians and reptiles, and the great morphological similarity, positions of organs, etc., and because *G. festina* Cordero, 1944, was reported from the biliary duct of its host, which is a common site of infection for dicrocoeliids, the author was in agreement with Byrd, Parker and others in placing *Glypthelmins* in the subfamily Brachycoeliinae; however, as stated above, because of the additional information contributed by recent life history studies the author has herein followed Johnston's suggestion in elevating Brachycoeliinae to familial rank. Furthermore *Glypthelmins* subscribes to the characteristics of Brachycoeliinae (now established as Brachycoeliidae) as given by Cheng (1957).

The difficulty in distinguishing *Glypthelmins* from *Margeana* has been recognized to be due to the unsatisfactory original generic characteristics, hence it is felt that a revision of these should be undertaken. The following is a revision of the generic diagnosis for *Glypthelmins* based on the combined observations of Stafford (1905), Miller (1930), and the author.

*Glypthelmins*.—Elongate distomes with spinous or aspinous cuticula. Anterior sucker subterminal; prepharynx and pharynx present; esophagus short to median length; conspicuous peripharyngeal glands present. Intestinal ceca long, bifurcating halfway between pharynx and acetabulum, reaching near posterior end of body. Acetabulum usually smaller than anterior sucker, never larger, situated mid-ventrally, in anterior  $\frac{1}{2}$  of body. Ovary and testes in anterior half of body; ovary anterior to testes, near acetabulum; testes oblique or side by side, situated near middle of body or slightly anterior. Conspicuous oötype, Laurer's canal, Mehlis' gland and seminal receptacle present. Long uterus, with ascending and descending loops accompanied by secondary transverse convolutions, reaching posterior end of body. Genital pore situated between crural bifurcation and anterior margin of acetabulum. Cirrus pouch, containing seminal vesicle and cirrus, situated on one side of acetabulum. Follicular vitellaria, extracecal and cecal and may join medially to fill medial plane of body; anterior and posterior boundaries limited to extent of ceca or less. Flame-cell pattern, according to Miller (1930) of  $2 \times 6 \times 3$  type. Large subterminal excretory opens ventrally.

*Type species*.—*Glypthelmins quieta* (Stafford, 1900) Stafford, 1905.

In the literature 16 species of flukes have been described as members of this genus; *G. quieta* Stafford, 1905; *G. linguatula* (Rud., 1819) Travassos, 1924; *G. parva* Travassos, 1924; *G. repandum* (Rud., 1819) Travassos, 1924; *G. elegans* Travassos, 1926; *G. staffordi* Tubangui, 1928; *G. palmipedis* (Lutz, 1928) Travassos, 1930; *G. californiensis* (Cort, 1919) Miller, 1930; *G. subtropica* Harwood, 1932; *G. rugocaudata* (Yoshida, 1916) Yahata, 1934; *G. shastai*



Ingles, 1936; *G. simulans* Texeira de Freitas, 1941; *G. proximus* Texeira de Freitas, 1941; *G. sera* Cordero, 1944; *G. festina* Cordero, 1944; and *G. africana* Dollfus, 1950. Among these only *G. quieta*, *G. subtropica* and *G. festina* subscribe to the generic characteristics in possessing peripharyngeal glands; the others are hereby transferred to the genus *Margeana*, except *G. africana* which is placed in *Reynoldstrema* n. gen.

The following are considered the only valid species of *Glypthelmins* basing the decisions strictly on morphological studies. Future life-cycle studies may again reduce some into synonymy.

All measurements given in millimeters.

#### GLYPTHELMINS QUIETA (Stafford, 1900) Stafford, 1905.

##### Plate 1, Fig. 1.

*Diagnosis*.—Elongate distome, 2.75-3.68 long, 0.88-1.5 wide. Cuticle aspinous according to Miller (1930) and spinous according to Stafford (1900). The 25 specimens studied by author showed no cuticular spines. Anterior sucker 0.26-0.35 in diameter. Acetabulum 0.18-0.21 in diameter. Prepharynx, pharynx and extremely short esophagus present. Two clusters of peripharyngeal glands seen on each side of pharynx. Ceca reaching posterior tip of body. Ovary approximately  $\frac{3}{4}$  size of testes, situated anterior-laterad to acetabulum in Miller's specimen, but postero-laterad and to left of acetabulum in type and author's specimens. Oötype, seminal vesicle, Laurer's canal present. Testes equal in size, lying side by side just posterior to ovary. Ascending and descending loops of uterus much convoluted transversely, limited to area between ceca. Vitellaria extra-cecal and cecal ranging from just posterior of crural bifurcation to immediately below testes (Miller, 1930). In specimens studied, vitellaria extend to near posterior tip of ceca.

*Type host*.—*Rana* spp.

*Type locality*.—Toronto, Canada.

Both Stafford (1900) and Miller (1930) failed to point out the presence of the seminal vesicle, oötype, Mehlis's gland, and delicate Laurer's canal which can be seen situated in the area just posterior to the ovary. The author has incorporated these organs in the generic characteristics for *Glypthelmins*. The question of spinous or aspinous cuticula cannot be solved at this time since Stafford's slides are no longer available. The 25 specimens studied did not reveal any cuticular spines. Perhaps an identical situation exists here as that described by Stafford (1903) in *Brachycoelium hospitale* (= *B. salamandrae*), where he at first (1900) described aspinous specimens and later (1903) found spinous specimens of the same worm.

#### GLYPTHELMINS SUBTROPICA Harwood, 1932.

##### Plate 1, Fig. 2.

*Diagnosis*.—Elongate oval body, 1.43-2.65 long, 0.44-0.92 wide. Cuticle spinous. Anterior sucker 0.16-0.32 by 0.18-0.34. Acetabulum 0.1-0.16 in diameter. Prepharynx, pharynx and esophagus present. Distinct peripharynx-

geal glands seen, extending to level of cecal bifurcation. Ovary 0.3-0.6 in diameter, situated on same level and to left of acetabulum. Elongate oval testes, 0.3 by 0.5. Uterine coils compactly interlocking, filling entire intracecal space, posterior to testes. Conspicuous metraterm, 0.005 long, present. Cirrus pouch with seminal vesicle and cirrus seen. Vitellaria occupying two lateral fields, from level of crural bifurcation to just posterior to testes; posterior to acetabulum, they extend mesiad to inner margin of ceca; anterior to acetabulum, they extend entirely across the worm. Eggs, 0.003 by 0.002 to 0.005 by 0.003.

*Type hosts.*—*Rana catesbiana*, *R. sphenoccephala*.

*Habitat.*—Small intestine.

*Type locality.*—Texas.

The type specimen, USNM Helminth. Coll. No. 30878 was studied. Brandt (1936) was able to identify *G. subtropica* from a collection of intestinal trematodes of *Rana catesbiana* from North Carolina, however Manter (1938) suggested and Rankin (1944) considered this species to be synonymous with *G. quieta*. The author feels that the distinct pattern of the vitellaria of *G. subtropica*, plus its reduction to approximately half the size of *G. quieta*, are of sufficient significance to separate it from the genototype.

#### GLYPHHELMINS FESTINA Cordero, 1944.

##### Plate 1, Fig. 3.

*Diagnosis.*—Elongate distome, 1.743-3.255 long. 0.693-0.966 side. Spinous cuticula. Anterior sucker 0.21 in diameter. Acetabulum 0.21 in diameter. Prepharynx, pharynx and esophagus present. Small peripharyngeal glands situated on each side of pharynx. Intestinal ceca only reaching to posterior  $\frac{1}{4}$  of body, distance from terminal tips of ceca to posterior end of body being 0.5-0.84. Suboval ovary, 0.21-0.275 by 0.145-0.23. Testes arranged tangentially, left one being slightly more anterior to its mate. Left testis, 0.38-0.4 by 0.275-0.42; right testis, 0.231-0.38 by 0.315-0.336. Uterine coils reaching posterior tip of body. Metraterm 0.315 long. Vitellaria, extracecal, cecal and slightly intercecal, extending from level of crural bifurcation to level of posterior testis. Eggs, 0.04 long.

*Type host.*—*Bufo arenarum*.

*Habitat.*—Biliary duct.

*Type locality.*—Montevideo, Uruguay.

The author is not in agreement with Babero (1951) who considered this species to be identical with *G. linguatula* (Rud., 1819), since, according to the revised diagnosis for the genus, *G. linguatula* should be transferred to *Margeana*. *G. festina* can be easily separated from *G. quieta* and *G. subtropica* by its shorter intestinal ceca and by its slightly overlapping testes which are diagonally arranged rather than side by side.

Of the three species of *Glyphelmins* now considered valid, only *G. quieta* and *G. subtropica* have ever been reported from North America.

## KEY TO THE GENUS GLYPHTELMINIS

1. Testes not situated side by side; intestinal ceca not reaching the posterior end of body, 0.5-0.84 mm. from posterior end .....*G. festina* Cordero, 1944.
2. Testes situated side by side; vitellaria never intracecal, nor joining in medial plane of body.....*G. quieta* (Stafford, 1900) Stafford, 1905.
3. Testes situated side by side; vitellaria extending and joining medially in area anterior to acetabulum and ovary....*G. subtropica* Harwood, 1932.

## Genus MARGEANA Cort, 1919.

The members of this genus are morphologically quite similar to the members of *Glypthelmins*; in fact, except for the absence of the prominent peripharyngeal glands as found in the latter, and a few other minor differences, there appear to be little difference between the two genera. For this reason Miller (1930) considered the two as synonymous. However, after reviewing the then described species, Miller stated: "A study of the descriptions of these species show that some of them do not fit the genus *Glypthelmins* as originally described by Stafford. Obviously then, this genus is in need of revision." The author has carefully studied all the original type descriptions and available type and paratype specimens, and feels that the best method of clarifying the '*Glypthelmins* complex' is to re-establish the validity of *Margeana*.

The revised diagnostic characteristics for *Margeana* are rewritten as follows:

*Margeana*.—Elongate distomes with spinous cuticula. Anterior sucker subterminal. Acetabulum in anterior  $\frac{1}{2}$  of body usually smaller than anterior sucker. Prepharynx present or absent; pharynx and short esophagus present. No peripharyngeal glands present. Intestinal ceca long, reaching to at least posterior  $\frac{1}{3}$  of body, usually reaching near posterior end. Ovary and testes in anterior half of body, with ovary situated near acetabulum anterior to and smaller than testes. Oötype, seminal receptacle, Mehlis' gland and Laurer's canal present. Uterus with descending and ascending loops accompanied by transverse coils, filling most of intracecal space limited to below level of testes in some, and not in others. Distinct metraterm present. Cirrus pouch situated lateral to acetabulum containing seminal vesicle, cirrus and prostate glands present. Genital pore immediately anterior to acetabulum. Follicular vitellaria extracecal and cecal, usually lying along a segment of the extent of ceca, but may fill areas lateral to pharynx and esophagus. Eggs operculate. Excretory pore subterminal. Parasites of intestines of amphibians.

*Type species*.—*Margeana californiensis* Cort, 1919.

Eleven species are being assigned to this genus as listed below. All measurements are given in millimeters.

## MARGEANA CALIFORNIENSIS Cort, 1919.

## Plate 1, Fig. 4.

Syn. *Glypthelmins californiensis* (Cort, 1919) Miller, 1930.

*Diagnosis*.—Body oval, covered with extremely fine cuticular spines except

in posterior 1/5 of body. Body length 2.4-5, width 0.64. Anterior sucker 0.4 in diameter. Acetabulum 0.24-0.31 by 0.25-0.41, situated anterior to testes. Prepharynx, pharynx and extremely short esophagus present; intestinal ceca reaching posterior end of body. Spherical testes, situated side by side, overlapping intestinal ceca dorsally along lateral borders. Spherical ovary approximately 2/3 diameter of testes, situated slightly posterior and on left of acetabulum. Inconspicuous seminal receptacle and oötype situated immediately posterior to ovary. Ascending and descending limbs of uterus intercoiled, filling all intracecal space posterior to testes. Vitellaria composed of small irregular follicles, located along each side of body, both dorsally and ventrally, and extending from level of anterior sucker to posterior margin of testes. Eggs operculated, 0.046-0.056 by 0.019-0.026.

*Type host.*—*Rana aurora*.

*Habitat.*—Small intestine.

*Type locality.*—California.

Three specimens of this species, recovered by the author from *Rana pipiens* in Virginia, were studied. Caballero and Sokoloff (1934) reported this species in *Rana montezumae* and *R. pipiens* from Mexico. Although Rankin (1944) considered *M. californiensis* (= *Glythelmins californiensis*) to be synonymous with *G. quieta*, the author is not in agreement since the absence of the peripharyngeal glands places *M. californiensis* in a different genus. In addition, the vitellaria of *M. californiensis* extend much further anteriorly than that of *G. quieta*. *M. californiensis* hence must be considered valid and is the generotype for *Margeana*.

### *Margeana linguatula* (Rud., 1819) n. comb.

Plate 1, Fig. 5.

Syns. *Distoma linguatula* Rud., 1819; *Glythelmins linguatula* (Rud., 1819) Travassos, 1924; *Haplometra palmipedis* Lutz, 1928; *Metorchis leptodactylus* Savazzini, 1930; *Glythelmins palmipedis* (Lutz, 1928) Travassos, 1930.

*Diagnosis.*—Elongate body, 3.35-8.68 long, 0.94-2.08 wide, with spinous cuticula. Anterior sucker with diameter of 0.29-0.73. Acetabulum, 0.22-0.4 in diameter. Prepharynx, pharynx and very short esophagus present. Intestinal ceca reaching near posterior end of body. Post-acetabular ovary, 0.25-0.53 by 0.27-0.55. Irregularly rounded testes, posterior to ovary, 0.27-0.60 in diameter, situated so that one is slightly anterior to its mate. Cirrus pouch large, averaging 0.8 by 0.13, containing conspicuous seminal vesicle and cirrus. Vitellaria extracecal and cecal, extending from level of esophagus to near posterior tips of ceca. Eggs, 0.025-0.034 by 0.013-0.017.

*Type host.*—*Cystignathus ocellatus*.

*Habitat.*—Intestine.

*Type locality.*—Brazil.

Although *M. linguatula* was the first species of the group to be described (Rudolphi, 1819), originally as *Distoma linguatula*, it was not until 1924 that Travassos transferred it to the genus *Glythelmins*. Since the author has straightened out the "*Glythelmins* complex"

by re-establishing *Margeana*, this species is assigned to the latter genus. *M. linguatula* can be separated from *M. californiensis* by its smaller testes which do not overlap the intestinal ceca, by its larger cirrus pouch, and by the extent of its vitellaria as described. Travassos (1924) reported this species from the same host plus *Bufo marinus*, *B. musicus* and *Ceratophrys cornuta* in Brazil.

Lutz (1928) described *Haplometra palmipedis* (Plate 2, Fig. 4) from the frog, *Rana palmipes*, Savazzini (1930) unknowingly described the same worm as *Metorchis leptodactylus*. Travassos (1930) was able to collect specimens of this species from *Bufo marinus*, *Leptodactylus ocellatus* and *L. caliginosus* from Caracas, Venezuela, S. Paulo and Salobra, Brazil, Montevideo, Uruguay, and Cordoba Province, Argentina. From his specimens he determined that *Haplometra palmipedis* should be transferred to the genus *Glypthelmins*. In clearing up the generic characteristics in this present study, and as the result of additional detailed morphological studies, the author places *G. palmipedis* as a synonym of *Margeana linguatula* (Rud., 1819). The body dimensions and the sizes and arrangements of the internal organs of *M. linguatula* and *G. palmipedis* are within the same ranges in some cases, and overlapping in others. The morphology and distribution of the vitellaria are identical. The few slight differences such as "subtriangular" testes in *G. palmipedis* is undoubtedly the result of fixation as is well known in helminthology. Travassos (1930) stated that the testes "in some specimens were slightly lobed," the "subtriangular" shape hence being inconsistent. Travassos also stated that the cuticle of *G. palmipedis* is aspinous. Possibly there are spinous and aspinous varieties; this alone certainly cannot be considered of value on the species level. The diagnosis given above incorporates the measurements portrayed by Travassos' specimens.

***Margeana repandum* (Rud., 1819) n. comb.**

Plate 1, Fig. 6.

Syn. *Distomum repandum* Rudolphi, 1819; *Glypthelmins repandum* (Rud., 1819) Travassos, 1924.

**Diagnosis.**—Elongate body with spinous cuticula, ranging from 3 to 10 (mean 4.5-5.6) long and averaging 1.4 wide. Anterior sucker 0.35 in diameter. Acetabulum 0.27 in diameter. Prepharynx absent, pharynx and extremely short esophagus present. Small oval testes, situated one anterior to its mate, 0.20-0.31 in largest diameter. Cirrus pouch with cirrus (0.2-0.24 long) and large seminal receptacle present. Ovary anterior to testes and posterior to acetabulum, 0.13-0.34 in diameter. Uterine coils intertwining and posterior to acetabulum, filling intracecal space. Vitellaria extracecal and cecal, follicles arranged in 12-15 grape-like clusters, limited anteriorly by posterior level of ovary and posteriorly in distal 1/6 of cecal length. Eggs 0.032-0.035 by 0.016-0.01.

**Type host.**—*Cystignathus ocellatus*.

**Habitat.**—Intestine.

**Type locality.**—Brazil.

Travassos (1924) reported this species in *Ceratophrys ocellatus* from Brazil. Because of the absence of peripharyngeal glands, *Glythelmins repandum* is transferred to *Margeana*. This species can be separated from *M. californiensis* and *M. linguatula* by the composition and arrangement of the vitellaria which are in grape-like clusters, and by their post-acetabular position. Rankin (1944) pointed out that the elongate body may be used as a diagnostic characteristic.

***Margeana parva* (Travassos, 1924) n. comb.**

Plate 2, Fig. 1.

Syn. *Glythelmins parva* Travassos, 1924.

**Diagnosis.**—Oval distome, averaging 1.3 long, 0.46 wide. Body covered with spinous cuticle. Anterior sucker 0.14 in diameter; acetabulum 0.13 in diameter. Prepharynx absent, large pharynx (0.1 by 0.12) and extremely short esophagus present. Ceca reaching near posterior end of body. Subspherical testes adjacent to one another, left one slightly anterior to right, measuring 0.15-0.17 in greatest diameter. Large cirrus pouch with cirrus and large seminal vesicle. Ovary with diameter approximately equal to that of acetabulum, partially overlapped by acetabulum and anterior testis. Ascending and descending loops of uterus intercoiled. Vitellaria extracecal and cecal, limited anteriorly by level of anterior border of acetabulum, posteriorly by level of posterior border of right testis. Eggs averaging 0.028 in length.

**Type host.**—*Cystignathus ocellatus*.

**Habitat.**—Intestine.

**Type locality.**—Brazil.

The author is not in agreement with Rankin (1944) in considering *M. parva* as synonymous with *Glythelmins quieta*, since the absence of peripharyngeal glands alone differentiates the two on the generic level. *M. parva* is different from *M. californiensis* and *M. linguatula* by the distribution of the vitellaria as described and by the distinct absence of a prepharynx. It can be separated from *M. repandum* by the extremely large conspicuous cirrus pouch and the bulbous muscular pharynx.

***Margeana elegans* (Travassos, 1926) n. comb.**

Plate 2, Fig. 2.

Syns. *Glythelmins elegans* Travassos, 1926; *Choledocystus elegans* (Travassos, 1926) Ruiz, 1949.

**Diagnosis.**—Body regularly elliptical with finely spinous cuticle; length 3.2-3.7, width 1.4-1.7. Anterior sucker 0.25-0.37 in diameter. Acetabulum 0.25-0.37 in diameter. Prepharynx absent, large pharynx, 0.17-0.25 in diameter, and short esophagus present. Intestinal ceca reaching near posterior end of body. Testes irregularly oval, situated far apart and on same level posterior to ovary and acetabulum, measuring 0.30-0.42 in greatest diameter. Large cirrus pouch, 0.70-0.82 by 0.17-0.20 lying to left of acetabulum. Ovary, par-



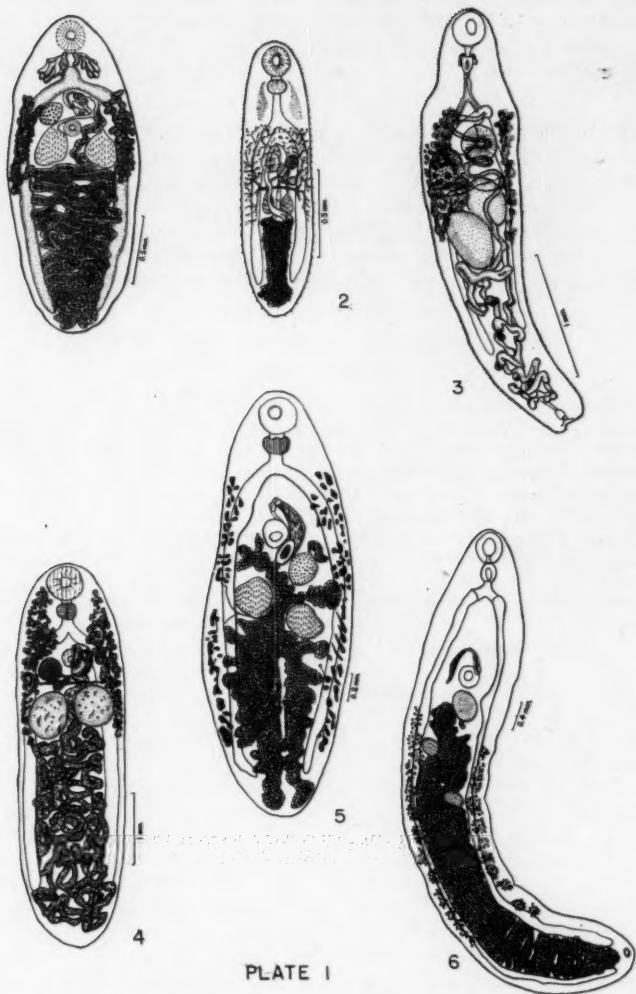


PLATE I

Figs. 1-5.—1. *Glyptelmins quieta* (Stafford, 1900). Stafford, 1905. (After Stafford, 1905). 2. *G. subtropica* Harwood, 1932. (After Harwood, 1932). 3. *G. festina* Cordero, 1944. (After Cordero, 1944). 4. *Margeana californiensis* Cort, 1919. (After Cort, 1919). 5. *M. linguatula* Rud., 1819 n. comb. 6. *M. repandum* Rud., 1819 n. comb. (After Travassos, 1924).



tially overlapped by acetabulum, lies immediately posterior to same, and is slightly smaller than testes in diameter. Uterine coils occupy all of intercecal, cecal and extracecal space posterior to level of acetabulum. Eggs operculate, 0.033-0.038 by 0.015-0.020. Excretory vesicle Y-shaped.

*Type host*.—*Leptodactylus ocellatus*.

*Habitat*.—Intestine.

*Type locality*.—Brazil.

Ruiz (1949) transferred this species to *Choledocystus* Pereira and Cuocolo, 1941, however Byrd (1950) correctly returned it to *Glypthelmins*. Since the generic characteristics of *Margeana* have been established. *G. elegans* is now known as *M. elegans* n. comb. This species can be separated from *N. californiensis*, *M. linguatula*, *M. repandum* and *M. parva* by the characteristic pattern of the vitellaria, and by the large area occupied by its uterine coils.

***Margeana staffordi* (Tubangui, 1928) n. comb.**

Plate 2, Fig. 3.

Syn. *Glypthelmins staffordi* Tubangui, 1928.

*Diagnosis*.—Elongate oval body, 2.09-4.15 long, 0.63-1.01 wide. Spinous cuticle. Anterior sucker 0.19-0.29 in diameter. Acetabulum 0.15-0.18 in diameter. Prepharynx, pharynx and short esophagus present. Intestinal ceca reaching posterior 1/5 of body. Rounded testes, 0.18-0.22 in diameter; left testis slightly more anterior than right. Large cirrus pouch, 0.26-0.33 by 0.06-0.09, antero-laterad to acetabulum. Rounded ovary, 0.13-0.18 in diameter, situated to left and on same plane as acetabulum. Uterine coils filling most of intracecal space behind level of testes. Vitellaria singularly follicular, strictly extracecal, reaching from anterior margin of acetabulum to last fourth of body. Eggs 0.031-0.033 by 0.015-0.018. Excretory vesicle Y-shaped.

*Type host*.—*Rana vittigera*.

*Habitat*.—Intestine.

*Type locality*.—Luzon, Philippine Islands.

This species has only been reported from the Orient. In addition to the original description, Syogaki (1937) reported it from *Rana augulosa* from Canton, China; and Yamaguti and Mitunaga (1943) redescribed it from the intestines of *Bufo melanostictus* in Formosa. Rankin (1944) believed that *M. staffordi* was identical with *Glypthelmins quieta*; however, in considering the revised generic characteristics, this cannot be possible. Tubangui (1928) stated that *M. staffordi* (= *G. staffordi*) could be separated from the other species by the extent of the vitellaria, arrangement of testes and ovary, and by the size of the eggs. The author, in an attempt to use the arrangement of testes and ovary in speciation, found that the slightly more anterior position of the ovary also holds true in other species in several cases, hence he concludes that this is undoubtedly an unreliable characteristic created during fixation. The author also found the overlapping dimensions of the eggs to be of no diagnostic importance. *M. staffordi*, however, can be separated from *M. cali-*

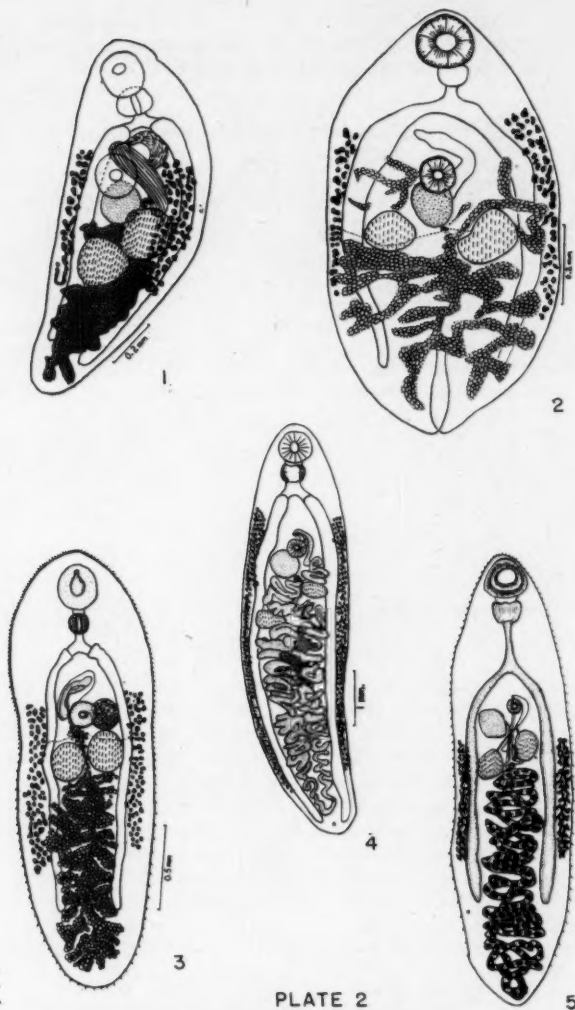


PLATE 2

Figs. 1-5.—1. *Margeana parva* Travassos, 1924 n. comb. (After Travassos, 1924). 2. *M. elegans* Travassos, 1926 n. comb. (After Travassos, 1926). 3. *M. staffordi* Tubangui, 1928 n. comb. (After Tubangui, 1928). 4. *M. linguatula* Rud., 1819 (= *G. palmipedia* Travassos, 1930). 5. *M. rugocaudata* Yoshida, 1916 n. comb. (After Yahata, 1934).

*forniensis*, *M. linguatula* and *M. repandum* by the arrangement of the vitellaria as described. It can be differed from *M. parva* by the size of its testes which are only  $\frac{1}{2}$  that of *M. parva*. *M. staffordi* can be separated from *M. elegans* by the location of its uterine coils which are not partially pre-ovarian nor extracecal.

***Margeana rugocaudata* (Yoshida, 1916) n. comb.**

Plate 2, Fig. 5.

Syns. *Enodiotrema rugocaudatum* Yoshida, 1916; *Glypthelmins rugocaudata* (Yoshida, 1916) Yahata, 1934.

**Diagnosis.**—Elongate distomes with spinous cuticula; 1.6-3.2 long; 0.7-0.9 wide. Anterior sucker 0.17-0.24 by 0.2-0.25. Small acetabulum 0.09-0.13 by 0.09-0.17. Prepharynx present; muscular pharynx 0.05-0.12 by 0.08-0.15; intestinal ceca reaching to posterior one-fourth of body length. Testes, 0.14-0.26 by 0.10-0.12, lying side by side behind ovary, but usually the one on same side as ovary situated slightly posterior to its mate. Fusiform cirrus pouch lying adjacent to acetabulum, opening at genital pore located immediately anterior to acetabulum. Ovary situated on either right or left of median line between testes and acetabulum, approximately same size as testes. Oötype, seminal receptacle and metraterm present. Ascending and descending loops of uterus are intercecal and intercoiling, reaching posterior end of body. No pre-testicular loops of uterus present. Extracecal follicular vitellaria limited to between levels of testes and just short of crural tips. Operculate eggs, 0.03-0.04 by 0.02-0.03.

**Type host.**—*Rana nigromaculata*.

**Type locality.**—Japan.

This species was originally described as a member of the genus *Enodiotrema* Looss, 1900, but was placed in *Glypthelmins* by Yahata (1934). Syogaki (1937) returned it to the original genus *Enodiotrema*. Rankin (1938) reconsidered the characteristics of this fluke and decided that it was synonymous with *Glypthelmins quieta*. In accordance with the generic characteristics proposed by this paper, the author must transfer this worm to the genus *Margeana*, since peripharyngeal glands are distinctly absent.

*M. rugocaudata* can be easily separated from the other members of this genus by the pattern of its vitellaria which do not extend anterior to the level of the testes. The author agrees with the return of this species to this complex since undoubtedly this worm more closely follows the description of *Margeana* than of *Enodiotrema* which are parasites of turtles.

***Margeana shastai* (Ingles, 1936) n. comb.**

Plate 3, Fig. 1.

Syn. *Glypthelmins shastai* Ingles, 1936.

**Diagnosis.**—Body elongate oval, 1.2-2.3 long, 0.54-0.77 wide. Anterior sucker 0.13-0.22 in diameter. Acetabulum 0.12-0.16 in diameter. Oval testes, 0.12-0.16 in diameter, obliquely arranged. Ovary 0.13-0.19 in diameter. Con-

spicuous seminal receptacle lateral to ovary. Short prepharynx, pharynx and esophagus (0.06-0.18 long) present. Ceca reaching posterior end of worm. Singularly follicular vitellaria, extracecal, cecal and intercecal, extending from level of genital pore to posterior 1/3 of body. Eggs, 0.031-0.032 by 0.014-0.017.

*Type host.*—*Bufo boreas*.

*Habitat.*—Intestine.

*Type locality.*—California.

The type specimen, USNM. Helminth. Coll. No. 8925 was studied. This species most closely resembles *M. linguatula* and *M. staffordi*, but it can be separated from the former by the absence of pre-testicular uterine coils, and from the latter by its vitellaria which are distinctly extracecal, cecal and intracecal, and by its naturally longer esophagus.

***Margeana simulans* (Texeira de Freitas, 1941) n. comb.**

Plate 3, Fig. 2.

*Syn. Glyphelmins simulans* Texeira de Freitas, 1941.

*Diagnosis.*—Irregularly oval body, averaging 2.51 long, 0.97 wide. Cuticle aspinous. Anterior sucker 0.25 in diameter; acetabulum 0.22 in diameter. Long prepharynx, inconspicuous pharynx (0.12 by 0.15) and extremely short esophagus present. Subtriangular testes obliquely situated; anterior testis (left), 0.20 by 0.30, posterior testis 0.25 by 0.33. Ovary 0.28 by 0.18. Small poorly defined seminal receptacle present. Uterine coils pre- and post-testicular. Eggs, 0.029 by 0.013.

*Type host.*—*Leptodactylus ocellatus*.

*Habitat.*—Intestine.

*Type locality.*—Montevideo, Uruguay.

*M. simulans* most closely resembles *M. linguatula* and *M. elegans*. Texeira de Freitas (1941) stated that *M. simulans* can be distinguished from *M. linguatula* by the relative positions of the acetabulum and the cirrus pouch. The author found the positions of the cirrus pouch to be of no value in speciation, however the acetabulum of *M. linguatula* is relatively more anterior than that of *M. simulans*, furthermore the inconspicuous pharynx and long prepharynx of *M. simulans* also serve as specific characteristics. It can be differed from *M. elegans* by the same characteristics.

***Margeana proximus* (Texeira de Freitas, 1941) n. comb.**

Plate 3, Fig. 3.

*Syn. Glyphelmins proximus* Texeira de Freitas, 1941.

*Diagnosis.*—Aspinous elongate body, 2.68-4.22 long, 0.74-1.0 wide. Anterior sucker 0.28-0.36 by 0.31-0.45. Acetabulum 0.13-0.25 by 0.17-0.25. Prepharynx, pharynx and short esophagus present. Ceca reaching near end of body. Rounded testes, obliquely placed, anterior testis (left) 0.28-0.31 by 0.23-0.30; posterior testis, 0.30-0.35 by 0.27-0.31. Ovary, 0.18-0.25 by 0.18-0.27.

Seminal receptacle and Mehlis' gland present. Ascending and descending loops of uterus not intercoiled. Extracecal and cecal vitellaria consisting of relatively small follicles extending from level of genital pore to 0.60-1.27 from posterior extremity. Eggs averaging 0.042 by 0.013.

*Type host*.—*Leptodactylus ocellatus*.

*Habitat*.—Intestine.

*Type locality*.—Montevideo, Uruguay.

*M. proximus* most closely resembles *M. shastai* and *M. rugocaudata*, however it can be differentiated by its non-intercoiling uterine loops, and its inconspicuous esophagus. It can be further separated from *M. rugocaudata* by its larger acetabulum and extent of its vitellaria, and from *M. shastai* by its distinctly smaller vitelline follicles which are not intracecal as in the latter.

#### *Margeana sera* (Cordero, 1944) n. comb.

Plate 3, Fig. 4.

Syn. *Glythelmins sera* Cordero, 1944.

*Diagnosis*.—Oval body elongate, 4.48 long, 1.2 wide. Anterior sucker 0.36 by 0.315. Acetabulum, 0.25 by 0.27. Oval testes obliquely arranged; left testis, 0.15 by 0.23, situated more anterior than right which averages 0.17 by 0.23. Ovary 0.315 in greatest diameter. Seminal receptacle (0.21 in diameter) and Mehlis' gland (0.105 in diameter) present. Prepharynx absent, pharynx and short narrow esophagus present. Intestinal ceca reaching posterior 1/3 of body, 1.26 from terminal end. Vitellaria consisting of grouped follicles, extracecal, extending from the level of ovary to near tips of ceca. Eggs, 0.035 in length.

*Type host*.—*Chthonerpeton indistinctum*.

*Habitat*.—Intestine.

*Type locality*.—Uruguay.

*M. sera* is most closely related to *M. rugocaudata* inasmuch as both species are distinct from the others in possessing shorter intestinal ceca and grouped vitelline follicles which occupy identical places. However *M. sera* can be differentiated from *M. rugocaudata* by having both pre- and post-testicular uterine coils, while *M. rugocaudata* possesses only post-testicular coils.

#### DISCUSSION

The last species of *Glythelmins* to be described is *G. africana* Dollfus, 1950 (Plate 3, Fig. 5), which by present diagnostic characteristics of the genus *Margeana*, should be transferred to it. However the type and paratype specimens, Nos. 23203, 23205, Museum national d'Histoire naturelle, Paris, both show testes which are situated in the posterior half of the body, while the uterine coils are mainly intercoiled in the posterior extremity of the worms, below the level of the cecal tips. These characteristics do not correspond to the diagnosis for *Margeana*, and hence the author does not feel it should be assigned

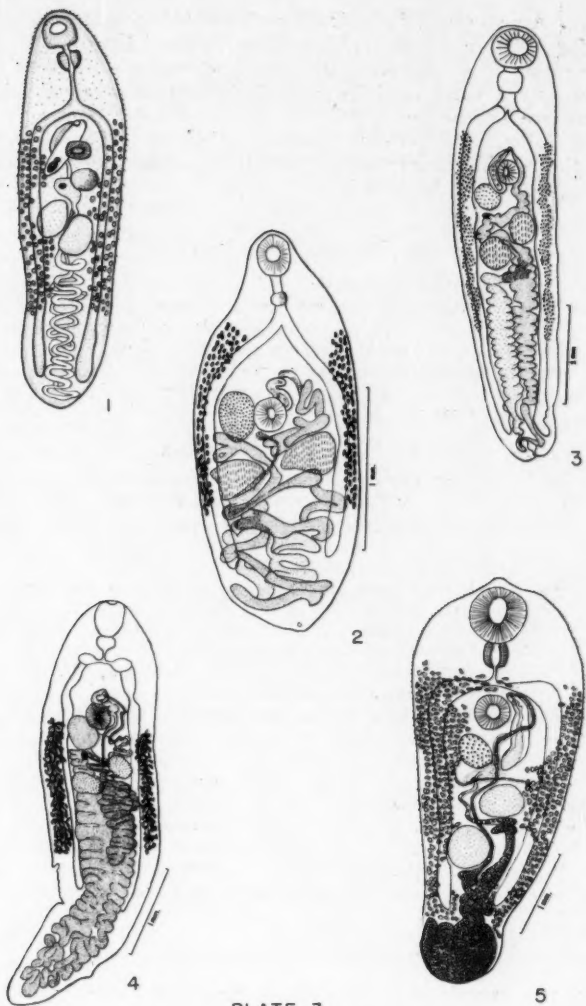


PLATE 3

Figs. 1-5.—1. *Margeana shastai* Ingles, 1936 n. comb. (After Ingles, 1936).  
 2. *M. simulans* Texeira de Freitas, 1941 n. comb. (After Texeira de Freitas, 1941). 3. *M. proximus* Texeira de Freitas, 1941 n. comb. (After Texeira de Freitas, 1941). 4. *M. seia* Cordero, 1944 n. comb. (After Cordero, 1944).  
 5. *Reynoldstrema africana* Dollfus, 1950 n.f. n. comb. (After Dollfus, 1950).

therein. A new genus *Reynoldstrema* is erected to include *R. africana* (Dollfus, 1950) n. comb. This will be discussed later.

Resulting from this systematic study, eleven species of *Margeana* are considered valid until further life-cycle studies can satisfactorily demonstrate differently.

The following key to the species of *Margeana* has been erected using the specific characteristics which the author feels are of sufficient consistency to be of value.

#### KEY TO THE GENUS *Margeana*.

1. Presence of pre-testicular uterine coils.
  - A. Vitellaria limited to between levels of anterior sucker and testes ..... *M. californiensis* Cort, 1919.
  - B. Vitellaria not extending anterior to level of ovary.
    - a. Intestinal ceca reaching to near posterior end of body ..... *M. repandum* (Rud., 1819) n. comb.
    - b. Intestinal ceca only reaching to posterior 1/3 of body ..... *M. sera* (Cordero, 1944) n. comb.
  - C. Vitellaria extending anterior to level of ovary.
    - a. Ascending and descending loops of uterus not intercoiling ..... *M. proximus* (Texeira de Freitas, 1941) n. comb.
    - b. Testes subtriangular, long prepharynx and obscure pharynx ..... *M. simulans* (Texeira de Freitas, 1941) n. comb.
    - c. Testes arranged approximately on same level.
      - i. Uterine coils diffuse, extracecal, cecal and intercecal; body half as wide as long; no prepharynx ..... *M. elegans* (Travassos, 1926) n. comb.
      - ii. Uterine coils intercecal, prepharynx present ..... *M. staffordi* (Tubangui, 1928) n. comb.
    - d. Testes not arranged side by side.
      - i. Obliquely arranged testes touching each other ..... *M. parva* (Travassos, 1924) n. comb.
      - ii. Testes obliquely arranged, not touching ..... *M. linguatula* (Rud., 1819) n. comb.
2. Absence of pre-testicular uterine coils.
  - A. Vitellaria extending anterior to level of ovary ..... *M. shastai* (Ingles, 1936) n. comb.
  - B. Vitellaria not extending anterior to level of ovary ..... *M. rugocaudata* (Yoshida, 1916) n. comb.

#### Genus REYNOLDSTREMA n. gen.

The new generic name is given in honor and in memory of the late Dr. Bruce D. Reynolds, Professor of Zoology, University of Virginia, and Past Director of Mountain Lake Biological Station, University of Virginia.

Dollfus (1950) described *Glypthelmins africana* from the intestines of *Rana mascareniensis* Dum. and Bibron, from a collection made by Prof. Paul Brien in 1937 from the Belgium Congo. Dollfus was



uncertain as to whether this trematode belonged to *Astiotrema* Looss, 1900, the members of which are typically parasites of chelonians, or *Glypthelmins* Stafford, 1905. The worm shows characteristics of both genera, but he concluded it must be a member of *Glypthelmins* because, "it is a parasite of *Rana* and none of the known members of *Astiotrema* has been found in a Batracien, I prefer to attribute it to the genus *Glypthelmins*, resembling *G. linguatula* (Rudolphi, 1819) L. Travassos, 1924, and *G. festina* E. H. Cordero, 1944.

Since this paper untangled the '*Glypthelmins* complex' by the re-establishment of *Margeana* Cort, 1919, to include all the species previously assigned to *Glypthelmins* but do not possess peripharyngeal glands, it seemed natural that *G. africana* should become *M. africana* (Dollfus, 1950); however, a careful study of the specimens as described by Dollfus revealed that this trematode does not subscribe to the generic characteristics of *Margeana* as given by the author, nor to the revised diagnosis of *Astiotrema* as given by Olsen (1937), since it does not portray a prepharynx, large seminal receptacle, long Laurer's canal, and stem of excretory bladder reaching seminal receptacle, which are the characteristics of *Astiotrema*. Its great similarity to *Brachycoelium*, *Glypthelmins* and *Margeana*, and its occurrence as an amphibian parasite, strongly suggests its membership in the family Brachycoeliidae. The posteriorly located uterus, and posteriorly situated testes are sufficient criteria to justify the erection of a new genus *Reynoldstrema*.

#### *Reynoldstrema* n. gen.

*Diagnosis*.—*Glypthelminae*. Elongate distomes, anterior end large and blunt, tapering to a small blunted posterior end. Spinous cuticula. Acetabulum smaller than anterior sucker. Prepharynx absent, pharynx and short esophagus present. Intestinal ceca reaching near posterior end of body. Post-ovarian testes diagonally arranged in posterior half of body. Large cirrus pouch containing large seminal vesicle and convoluted cirrus, extends posteriorly beyond acetabulum to level of ovary. Ovary post-acetabular and submedial in anterior half of body. Small seminal receptacle, inconspicuous Mehlis' gland and Laurer's canal present. Uterus with ascending and descending loops reaching posterior end of body, main body of which situated in intracecal and post-testicular space. Vitellaria extending along length and around tips of ceca. Eggs operculated. Parasites of intestines of amphibia.

*Type*.—*Reynoldstrema africana* (Dollfus, 1950)

So far only one species, *R. africana*, which can be assigned to this genus, has been described in the literature. All measurements are given in millimeters.

#### *Reynoldstrema africana* (Dollfus, 1950) n. comb.

Plate 3, Fig. 5.

*Diagnosis*.—Elongate distome with blunted ends, larger anteriorly. Cuticle spinous. 3.46-3.58 long, 1.199-1.279 wide. Oral sucker 0.425-0.438 by 0.438-

0.499. Prepharynx absent, pharynx and inconspicuous esophagus (0.064-0.116 long) present. Acetabulum 0.245-0.258 by 0.258. Anterior testis (left), 0.375-0.380 in diameter; right testis, 0.375-0.385 in diameter. Large cirrus pouch, 0.141-0.167 in diameter, present. Oval ovary, 0.27-0.28 in diameter. Vitellaria, extracecal, cecal and intercecal, extending from level of crural bifurcation to around tips of ceca. Eggs, 0.031-0.036 by 0.019-0.022.

*Type host*.—*Rana mascareniensis*.

*Habitat*.—Intestine.

*Type locality*.—Sakania, Belgium Congo.

#### SUMMARY

The '*Glyphelmins* complex' is divided into two genera, *Glyphelmins* Stafford, 1905 and *Margeana* Cort, 1919, using the presence and absence of peripharyngeal glands as the main differentiating criterion. The diagnoses of the two genera are revised and keys to the valid species are given.

*Glyphelmins* now includes *G. quieta* (Stafford, 1900) Stafford, 1905; *G. subtropica* Harwood, 1932; and *G. festina* Cordero, 1944. *Margeana* now includes *M. californiensis* Cort, 1919; *M. linguatula* (Rud., 1919) n. comb.; *M. repandum* (Rud., 1819) n. comb.; *M. parva* (Travassos, 1924) n. comb.; *M. elegans* (Travassos, 1926) n. comb.; *M. staffordi* (Tubangui, 1928) n. comb.; *M. rugocaudata* (Yoshida, 1916) n. comb.; *M. proximus* (Texeira de Freitas, 1941) n. comb.; and *M. sera* (Cordero, 1944) n. comb. *Glyphelmins palmipedis* (Lutz, 1928) Travassos, 1930, is reduced to synonymy with *M. linguatula*.

*Reynoldstrema* n. gen. is erected to include *R. africana* (Dollfus, 1950) which although closely related, does not satisfy the characteristics of either *Glyphelmins* or *Margeana*.

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## The Disappearance of an Area of Prairie in the Cook County, Illinois, Forest Preserve District<sup>1</sup>

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Typical prairie and characteristic forest occur within a few feet of each other. Climatic factors cannot be used to explain the differences. Drainage, fire, and grazing are factors in determining which shall be present, forest or prairie; but taken separately or together, they do not give the answer to the question. Cowles (1929) states that the presence of forest or prairie rests on factors starting in the past and continuing to the present with cumulative differences, especially in soil. This is only a partial truth. In his lectures Cowles often pointed out that tree seeds do not germinate and seedlings survive in prairie. Soil studies have afforded evidence that over long periods of time with climatic changes, forest has invaded prairie and prairie has invaded forest. Devious patterns of forest and prairie soil occur in areas from which forest has been removed. Speaking in terms of a few centuries, prairies are doubtless as persistent as Cowles (1929) assumed.

There was no evidence of any invasion of prairie by woody plants in 1905 through 1915 in the area shown in Fig. 1, and there is no reason to assume that there had been any appreciable change in the wood's edge for at least a century, or perhaps much longer. The area is a part of a practically continuous prairie, reaching west nearly to the Mississippi River, interrupted only by stream-skirting forest and groves. The tract, shown in the photographs, out to the tip of the forested parts contains about three acres of prairie. It is located east of the Chicago Zoological Park (Brookfield, Illinois), between First Avenue and the Des Plaines River, and south of Thirty-first Street. Approximately two acres of the prairie area were purchased by the Cook County Forest Preserve in 1917. The limits of the original forest can be determined by the location of the large old oaks and other trees along the south and east, but not the north, margin of

<sup>1</sup> The writers wish to thank Roberts Mann and David Thompson of the Cook County Forest Preserve District for assistance in various fields and Dr. A. G. Vestal for advice. The study of grasses by Paul C. Lemon, made in 1935, proved very important. The Illinois State Museum and the Department of Zoology, University of Illinois, furnished transportation, drafting, photography and typing. W. B. MacCollum assisted with the 1907, and E. H. Bennett with the 1947 photography.

what was once prairie (Fig. 1). The forest at the left (SW) of Fig. 1 was continuous with the flood plain forest of Salt Creek. A photograph, looking northeasterly from the location of the line marking the short transect across the edge vegetation (Fig. 3), shows a good forest edge vegetation on the north and in the northeast corner (Shelford 1920, Fig. 10). At the point on Fig. 3 marked for a dogwood shrub there was almost none of the forest edge plants. Light tolerant forest floor plants merged with the prairie vegetation. How far north this extended is not known. Likewise there are no known records of any kind of quantitative study or mappings of plants in the area.

The important plants of the prairie vegetation are: big bluestem (*Andropogon furcatus*)—common; little bluestem (*A. scoparius*)—less common than *A. furcatus*; June grass (*Koeleria cristata*)—in patches; dropseed (*Sporobolus heterolepis*)—common; Indian grass (*Sorghastrum nutans*) and wheat grass (*Agropyron repens*). These occur throughout the local prairies. The list is by Paul C. Lemon from observations made Oct. 4, 1935 in the area to the right of center in Fig. 1 where the *Silphiums* are absent. Probably an examination of this spot in 1907 would have shown it to be high prairie, which has abundant little bluestem, few *Silphiums* and several species of *Solidago* and *Aster*; *Stipa spartea* is commonly present. In the low



Figs. 1 and 2.—1. (Left) Portion of a photograph looking in a north-westerly direction from the location of the square black dot in Fig. 3, taken in June 1907; located due west of the center of Riverside, Illinois near  $41^{\circ} 50' N.$ — $87^{\circ} 50' W.$ , and known locally as the Riverside prairie. One-third of the length of the photograph is cut off at the right; it showed solid forest in the background but no additional features in the prairie, (See Shelford 1920, Figs. 10 and 12). 2. (Right) Photographed in June 1947, looking in the same general direction from the same spot. The trees shown in Fig. 1 were removed, probably about 1926, and since that date the area has been overgrown with hawthorn. The lower part is the second exposure to show what is left of the prairie vegetation—compass plant and prairie onion are nearly absent. There is only a little grass. By 1955 this area was materially reduced to size.



prairie appears compass plant (*Silphium laciniatum*) whose divided leaves face the rising sun, rosin weed (*S. terebinthinaceum*) and wild onion (*Allium cernuum*) which provides the ball-like white flowers (Fig. 1). There is usually much big bluestem and sometimes cord grass (*Spartina pectinata*).

Vestal's studies (1914), made six miles northwest from the area being considered, contributed much of the information on northern Illinois prairie and forest edges. An edge is composed of small trees, outside of which there are shrubs, followed by forbs adjacent to the grasses. The small trees are *Malus*, *Crataegus*, and *Prunus*.

The invasion of the prairie has taken place in two main ways: (a) by scattered growth of trees and shrubs in the grass area, and (b) by invasion of the grass by the edge organisms. The latter is a mass movement of plants and animals into the grassland and has taken place perhaps only in the southeast corner of the area. Here it appears that it has been caused by reduced sunlight due to shade of the hawthorn thicket to the south and increased height of the surrounding trees. The hawthorn thicket was a completed invasion at least twenty years ago.

A rough transect about one meter wide was studied as indicated by the black line in the lower left corner of Fig. 3. The first tree in the edge of the woods outside the oaks is a black cherry (*Prunus serotina*). Beginning near the cherry tree, a distance of 28 meters was censused. The first 7 meters contained small hawthorn trees (*Crataegus mollis*), a small crabapple tree (*Malus ioensis*) small white ash trees, and some hazel (*Corylus americana*). The second 7 m was nearly pure hawthorn which ended the first 14 m. The next 3 m (15th - 17th) contained 32 sunflowers (*Helianthus grosseserratus*), 32 goldenrods (*Solidago glaberrima*), 10 tall tickseed plants (*Coreopsis tripteris*), 2 *Aster* spp. and 1 rosin weed (*Silphium terebinthinaceum*). The 18th-24th m were almost pure *Aster prealtus*. The 25th m was almost pure tickseed (*Coreopsis tripteris*). The 26th - 28th m contained willow, some rosinweed, and scattered plants of the prairie. Here the transect ended (Sept. 28, 1953).

In the final remaining prairie there were fewer plants of Indian grass (*Sorghastrum nutans*) than of switch grass (*Panicum virgatum*). Rosin weed, or the entire leafed silphium, was a predominant species. One compass plant was found; *Solidago rigida* was scattered throughout; there was also a single plant of rattlesnake master (*Eryngium yuccifolium*) and tall tickseed (*Coreopsis tripteris*). There were non-fruited clumps of grass, probably one or both of the andropogons, American feverfew (*Parthenium integrifolium*), and black-eyed susan (*Rudbeckia hirta*). Many of the plants mentioned were found near Elmhurst by Vestal (1914). This group has been invading the prairie area which was obviously smaller in 1954 than in 1947 when Fig. 2 was photographed. The surrounding hawthorns have grown considerably since 1947.

The cause of the row of even-aged hawthorns suggests that a

stray deer, a heavy man, or a horse and rider crossed the area of the row of hawthorns, and pressed hawthorn seeds through the sod, so that some of them could germinate and grow. The late Professor F. C. Gates stated (personal communication) that he found seedlings of forest edge shrubs growing in cow tracks in Kansas prairie. The growth of trees among the grasses was evidently not due to soil disturbance. Part of this area and the land to the north was laid out in curvilinear streets about 1870. One of these entered the prairie and the grading of a narrow road can be seen; but by 1907 it had grown up to prairie so completely as not to show in the photograph. The 1870 sewers and drains north of Thirty-first Street evidently did not seriously affect the prairie.

The change in the prairie began in the late 1920's, with general disturbance. The years 1926 to 1930, 1933 and 1937 were characterized by the construction of the Chicago Zoological Park, the building and widening of the First Avenue pavement, and the building of the Thirty-first Street bridge (1931). Mosquitoes were numerous in 1926 and mosquito abatement began and continued undirected for several years. The large trees shown in Fig. 1 were removed and are in part replaced by sprout trees 4 to 5 inches in diameter in 1956. In 1905 First Avenue was a dirt road which was macadamized some time later. This was replaced by a pavement which sloped to the west and drained into a catch basin near the south side of the prairie area; the basin drained into the river. On or before 1934 the mosquito abaters made a ditch about two feet deep east of the shoulder of the First Avenue pavement. The ditch drained to a point a little south of the prairie and thence to the river. There is some evidence that a shallow mosquito ditch was made across the area soon after 1934.

In 1927 the main body of the original prairie was in good condition, but a very few hawthorns were noticeable along its north edge. By 1937 these or other woody plants were generally distributed except in the sparsely invaded area and the southeast corner. It is evident that the prairie soil was gradually dehydrated between the early 1920's and the early 1950's. The southeast corner suffered least because the surface of the small prairie-covered area is a depression perhaps 2-4 inches below the surrounding area, not found by the mosquito abaters. The invasion of the prairie by scattered trees and shrubs was without doubt largely due to a general lowering of the water table and weakening of the grasses.

When there are young trees and shrubs in a prairie area, more mammals can reside there and birds can perch; their effect is increased and the invasion becomes an autoaccelerated process. David Thompson reports mammals and birds are abundant in the present hawthorn grove. We found a quail dusting site and abundant raccoon signs. Birds and mammals often eat seeds, and Krefting and Roe (1949) point out that the seeds of hawthorn are rendered more viable by passing through alimentary tracts of turkeys. These authors report better germination in smooth sumac (*Rhus glabra*) and wild rose

after ingestion by birds, but dogwood and cherry seeds are injured.

Where the invading trees were sparse (Fig. 3), the plants listed below were present in 1954. This area is separated from the remaining prairie by a tongue of forest trees. In the sparse area the scattered trees were *Crataegus* and *Malus* and a very few sumac. In the lower story there was scattered *Rosa blanda*, some blue grass (*Poa pratensis*), bottlebrush grass (*Hystrix patula*), tall tickseed (*Coreopsis tripteris* probably common in north-facing edges) and *C. palmata*, American feverfew (*Parthenium integrifolium*), flowering spurge (*Euphorbia corollata*), cup plant (*Silphium perfoliatum*), spreading dogbane (*Apocynum androsaemifolium*), and a few scattered lead plants (*Amorpha canescens*).

The officials of the Cook County Forest Preserve are positive that there has been no fire in the area since 1930. Young hawthorns are killed completely by intense fire, and larger well-established ones are killed above the ground but commonly send up new plants sometimes 12 to 15 feet away (R. W. Lorenz, personal communication). There is no evidence that root sprouts were a factor in this case. The officials also believe that frequent burning of the prairie would have saved it. This may be true, especially if the mosquito ditch had not been dug. If fire had been applied, the lowering of the water table which took place to some extent before the ditch was made would probably have resulted in a prairie with goldenrod and *Stipa spartea*.

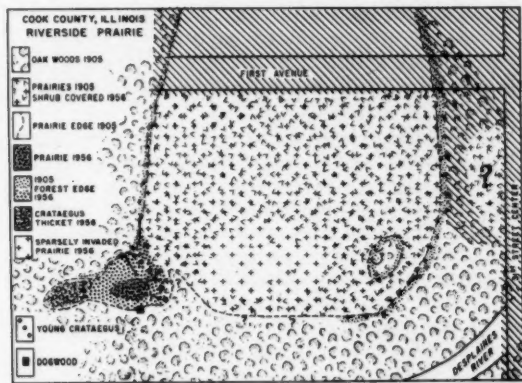


Fig. 3.—A diagram of the prairie area; to the right is north. The oblique ruling shows where the natural vegetation of both forest and prairie has been destroyed or greatly modified; outside this area, the forest remains as in 1905. Nearly all the prairie is taken over by crab apple and hawthorn (vaguely suggested by the crosses) and sumac and bur oak (more vaguely by the Vs). The black line near the 1956 prairie is the transect described in the text. The crataegus circles are those noted in the text and conspicuous in 1953. The dogwood is important as a very late edge arrival on the camera site of 1907 and 1947. The prairie is shown as of 1953, much smaller than in 1947.

There is a consensus of opinion among those who are planning on protecting prairie that burning should take place about every three years. This should be one third each year to retain and protect the animals. The purpose in general is to remove the accumulated plant material. The pulling of tree seedlings in their first spring, while the grass is brown and the seedlings green, is easy.

The deciduous forest edge is a type of vegetation characteristic of regions in the westward fingering of forest along streams into the western plains (Aikman, 1926; Weaver, Hanson and Aikman, 1925). The edges of northern Illinois were doubtless in the same position for a very long period before white settlement. In northeastern Nebraska none of the small trees of the edges under consideration are of any importance in edges. There the edges are usually of hazel next to the woods with smooth sumac well out next to the grasses and some coralberry (*Symphoricarpos orbiculatus*) between the two. In the area of study where drainage is most intensive near the First Avenue mosquito ditch, the area is covered with smooth sumac, a disturbance plant, probably not in natural forest edges in Illinois. In the probably former grassland area near Thirty-first Street (Fig. 3), there are a number of depressions a few inches deep and about 10 m in diameter. There is a circle of hawthorns with another circle of sumac inside on the lower ground. This suggests a lowering of the water table and the initiation of a more arid condition. This peculiar arrangement of sumac and hawthorn probably represents two stages in dehydration of the soil. Two midwestern plants, wild hyacinth (*Camassia scilliioides*), and yellow pimpernel (*Taenidia integerrima*) were present (May, 1956). Bur oak has invaded the hawthorn-crab apple area along with one or more individuals of other forest trees.

Study of the interactions of the edge plants in eastern Nebraska shows that hazel is the aggressive species (Clements, Weaver and Hanson, 1929). Studies of natural edge vegetation in Illinois are inadequate for definite conclusions but hawthorn appears to be the aggressive species. Lack of edge study is unfortunate as it can throw much light on the migration of communities. Under human occupation there appears to be a widespread tendency for forest to invade prairie (Fitch and McGregor, 1956).

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## Soricidae of Arizona

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A number of records not heretofore reported and a lack of distributional data of Arizona soricids prompted the author to report on the distribution of Soricidae in Arizona using all available records.

Insectivores in Arizona are represented by five species of shrews: *Sorex vagrans monticola* Merriam, *S. merriami leucogenys* Osgood, *S. nanus* Merriam, *S. palustris navigator* (Baird), and *Notiosorex crawfordi crawfordi* (Coues). *S. vagrans* is represented by 126 specimens, *S. merriami* by six, *S. nanus* by two, *S. palustris* by three, and *Notiosorex* by 27.

Each species account consists of the altitudinal range, geographical distribution, ecological distribution, and records of occurrence. The following abbreviations are used with the records of occurrence: BS . . . United States Fish and Wildlife Service, Biological Survey Collections, Washington, D. C. Carnegie . . . Carnegie Museum, Pittsburgh, Pennsylvania. CMNH . . . Chicago Museum of Natural History. MVZ . . . Museum of Vertebrate Zoology, University of California, Berkeley. RWD . . . collection of Robert W. Dickerman. SDSNH . . . San Diego Society of Natural History, San Diego, California. UA . . . Department of Zoology, University of Arizona, Tucson. UI . . . Department of Zoology, University of Illinois, Urbana. UM . . . Department of Zoology, University of Michigan, Ann Arbor. A distribution map for each species and a master locality map (Fig. 1) are included within the body of the report.

*Acknowledgement.*—This paper was originally suggested by Dr. E. Lendell Cockrum, Department of Zoology, University of Arizona to whom I am indebted for supplying the records of occurrence and for reviewing the manuscript. Dr. Charles H. Lowe, Jr., Department of Zoology, University of Arizona, gave helpful information. The two photographs of the Superior area were taken by R. R. Crosby. J. A. Munro supplied the Santa Catalina Mountains, Bear Canyon, *Notiosorex* record. Mrs. Susan Slutes, the secretary of the University of Arizona Department of Zoology, typed the manuscript.

### ACCOUNTS OF SPECIES

#### *Sorex vagrans monticola* Merriam

*Altitudinal range.*—6,000-11,500 feet.

*Distribution.*—The vagrant shrew is known from Tunitcha Mountain (a peak in the Chuska Mountains) in northeastern Apache County, the Mogollon Rim country, and isolated mountain ranges in southeastern Arizona. Since damp areas are the preferred habitat, this



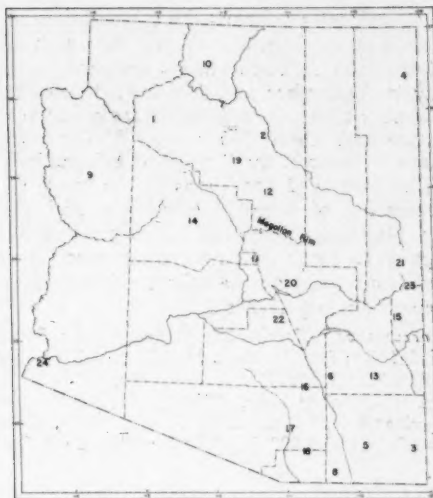


Fig. 1.—Master locality map, arranged alphabetically as follows: (1) Aubrey Cliffs, (2) Black Falls Indian Ruins, (3) Chiricahua Mts., (4) Chuska Mts., (5) Driagon Mts., (6) Galiuro Mts., (7) Grand Canyon, (8) Huachuca Mts., (9) Hualpai Mts., (10) Kaibab, (11) Maazatzal Mts., (Mogollon Rim), (12) Mormon Lake, (13) Pinaleno (Graham) Mts., (14) Prescott, (15) Rose Peak in the Blue Range, (16) Santa Catalina Mts., (17) Santa Cruz River, (18) Santa Rita Mts., (19) San Francisco Mts., (20) Sierra Ancha Mts., (21) Springerville, (22) Superior, (23) White Mts., (24) Yuma.

shrew is limited to the higher and cooler elevations of the state. Its distribution thus corresponds closely with that of forest trees (Fig. 2). On the basis of the habitat preferences indicated by the present records, *S. vagrans* may be expected in the Kaibab country, Grand Canyon, Aubrey Cliffs, Hualpai Mountains, the Prescott area, Mazatzal Mountains, Sierra Ancha Mountains, Galiuro Mountains, and some other isolated ranges in the southeastern part of the state. Lack of collecting may account for its apparent absence in some of these areas.

The vagrant shrew has been taken in southeastern Arizona near a stream on a yellow-pine slope in the Catalina Mountains; in horsetail (*Equisetum*) by a spring in deciduous woodland (Hoffmeister and Goodpaster, 1954); among grass along streams in high meadows and along a wooded stream at 6,000 feet (Hoffmeister, 1956b); under brush along a creek in fir and spruce country (Hall, 1932); and along a stream at 9,000 feet in Long Park (Cahalane, 1939).

Clothier (1955) found *S. v. monticola* most common in similar habitat in western Montana. Dalquest (1948) found *S. vagrans* in marshy areas from Upper Sonoran through Canadian life-zones. The

subspecies, *S. v. halicoetes*, inhabits the salt marshes of San Francisco Bay; temperatures range from 28° F. to a rare high of 100° F., with an average of about 55°. These shrews are probably exposed to arid conditions only in September and October: 18 to 25 inches of rain falls from November to April, and high tides occur in the intervening months (Johnston and Rudd, 1957).

Climatic data for some of the *S. vagrans* Arizona localities are given in Table I. The most arid conditions in the range of *S. vagrans* in Arizona (combination of lowest precipitation and highest temperature) occur in May and June, and possibly again in September or October in part of its range. The breeding season is not known, but it is interesting to speculate on the effects (if any) that aridity might have on the reproductive period(s).

*Records of occurrence.*—Total, 126: Coconino Co.: San Francisco Mts., 8,000-11,500 ft., 3 (BS); San Francisco Mts., 6 (CMNH); Little Spring, San Francisco Mts., 8,000 ft., 1 (MVZ); Bakers Butte, 8,000 ft., 5 (MVZ); Sawmill Spring, 8 m. SE Mormon Lake, 7,300 ft., 1 (MVZ). Navajo Co.: Buck Springs, Buck Springs R.S., 18 m. SE Bly R.S., 2 (UA). Apache Co.: Spruce Creek, Tunitcha Mt., 7,800-9,000 ft., 7 (BS); Wheatfield Creek, 7,000 ft., 1

TABLE I.—Climatic data for some Arizona *Sorex vagrans monticola* localities (from Smith, 1956)

Station	Length of period (approx. in some cases)	Elevation (feet)	Ex- treme temp. (F°)	Mean temp. (F°)	An- nual ppt. (inches)	Months with less than 1" ppt.
Alpine	1912-53	8,000	-29 to 92	43.4	22.3	Apr May Jun.
Flagstaff	1898-53	6,993	-30 to 93	45.7	20.0	May Jun.
Heber R. S.	1916-36 1948-53	6,600	-28 to 97	47.6	17.8	May Jun. Oct.
Mt. Lemmon (Catalina Mts.)	1950-53	7,690	5 to 87	49.6	27.9	Feb. May Jun. Sep.
Wallace R. S.	1939-53	7,006	-22 to 96	47.6	18.0	May Jun.
Williams	1906-53	6,750	-25 to 99	48.4	21.7	May Jun.

(BS); Springerville, 6,700 ft., 2 (1, BS; 1, MVZ); W. Fork Black R., White Mts., 7,800 ft., 2 (UA); Horseshoe Cienega, White River, White Mts., 8,300 ft., 5 (BS); north fork, White River, White Mts., 12 (SDSNH); near head Burro Creek, White Mts., 9,000 ft., 1 (BS); Little Colorado River, White Mts., 8,300 ft., 4 (BS); Sheep Crossing, Little Colorado R., White Mts., 9,500 ft., 1 (UA); Mt. Thomas, 9,500-11,000 ft., 12 (BS); Reservation Creek, 9,600 ft. [S. side Mt. Thomas], 1 (MVZ); near Boat Landing, Big Lake, White Mts., 1 (RWD); W. fork Black River, 7,500-7,700 ft., 2 (MVZ). *Greenlee Co.*: Hannagan Creek, 8,600 ft., 11 (MVZ); Hannagan Meadows, 9,500 ft., 6 (MVZ); Prieto Plateau, S. end Blue Range, 9,000 ft., 1 (BS); Rose Peak, 8,700 ft., 2 (MVZ). *Graham Co.*: Graham Mts.: Marijilda Canyon, 8,600 ft., 5 (MVZ); near head Ash Creek, 9,200 ft., 2 (BS). Additional records from Hoffmeister, 1956: 265: Graham Mts.: Hospital Flat, 9,000 ft., 2; Snow Flat, 8,750 ft., 2; 1/3 m. W. Columbine R.S., 9,400 ft., 1; Soldier Creek, 9,400 ft., 1; Treasure Park, 8,950 ft., 1; Wet Canyon, 6,050 ft., 1. *Pima Co.*: Santa Catalina Mts.: Summerhaven, 7,500 ft., 4 (3, BS; 1, SDSNH); Soldier Camp, 1 (Carnegie); Carter Canyon, 1 (UA). *Santa Rita Mts.*: Boulder Spring, Santa Rita Range Reserve, 1 (UA); Stone Cabin Canyon, 8,500 ft., 1 (BS). *Cochise Co.*: Huachuca Mts.: 1 (BS); 7,500 ft., 1 (Carnegie); Miller Canyon, 5 (UI). *Chiricahua Mts.*: Fly Park, 4 (BS); Long Park, 9,000 ft., 1 (UM); Rustler Park, 1 (SDSNH).

#### *Sorex merriami leucogenys* Osgood

*Altitudinal range.*—about 7,000-9,000 ft.

*Distribution.*—Six specimens of Merriam's shrew have been col-

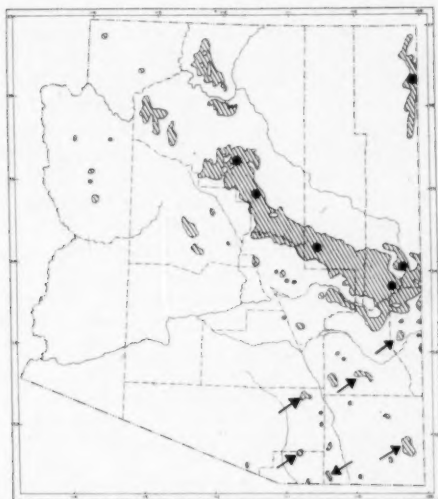


Fig. 2.—Distribution of *Sorex vagrans monticola* in Arizona. Records of occurrence are indicated by dots and arrows. Hatched area shows the distribution of forest trees, mainly yellow pine (from Nichol, 1952).

lected in Arizona (Fig. 3). *S. m. leucogenys* and *S. v. monticola* have been taken together at Sawmill Springs and Rose Peak. Hall (1933) reproduces the field notes of Miss Annie M. Alexander, the collector of the Sawmill Springs *S. m. leucogenys*: "taken at root of willow in thicket of rush, grass, lupines, solomon-seal, violet, wild rose; three feet from water." Yellow pine and trembling aspen (*Populus tremuloides*) were the dominant trees (Hall, *loc. cit.*). The habitat of the Rose Peak specimen is not known to the author, but as Hoffmeister points out (1955), it must be in the Transition life-zone or higher. The other four specimens of Merriam's shrew come from Grand Canyon National Park: three from ponderosa pine country on the South Rim, and one from a grassy meadow in spruce-fir country on the North Rim (Hoffmeister, 1955). *S. m. leucogenys* and *S. v. monticola* may occur sympatrically over a greater area than is presently indicated. The factors isolating these two forms in Arizona are not known.

Additional *S. merriami* records from relatively moist habitats are as follows: the first Merriam shrew recorded from New Mexico, taken at 8,300 feet in a grassy meadow near a white fir (*Abies concolor*) forest (Findley, 1956); a Wyoming specimen trapped along a drainage ditch with little vegetative cover (Mickey and Steele, 1947); and a Montana shrew from a timothy field adjacent to a creek bordered by ponderosa pine, Douglas fir, and trembling aspen. *S. merriami* records from such areas are unusual. Jackson (1921; 1928) states that these shrews are atypical of other American shrews of the genus *Sorex* in that they are found in arid regions. Such is the case with the Merriam shrew specimens of the subspecies *merriami* reported from California (Benson and Bond, 1939); the California specimen of the subspecies *leucogenys* trapped at 9,500 feet in sagebrush (Hoffmann, 1955); the Utah specimens of the race *leucogenys* taken in a high, dry, grassy meadow (Durrant and Lee, 1955); the Nevada specimen, race *merriami*, collected in a rocky, hilly area supporting sagebrush and rabbit-bush (McNab, 1954); two Colorado specimens (Hoffmeister, 1956a; Starrett and Starrett, 1956); a Montana specimen trapped in a *Microtus* runway in a grassy, weedy fence-row (Hooper, 1944); and three Washington shrews, subspecies *merriami*, one taken on a grassy hill at 645 feet elevation and two taken in sagebrush, one of these trapped in the burrow of *Lagurus curtatus pauperrimus* (James, 1953).

*Records of occurrence.*—Total, 6: Coconino Co.: 5 mi. N., 1 m. E. Bright Angel R.S., 1 (UI); Grand Canyon Village, 1 (UI); Long Jim Canyon, 3 m. S., 4 m. E. Grand Canyon Village, 1 (UI); Buggelin Tank, 5½ m. S., 10½ m. E. Grand Canyon Village, 1 (UI); Sawmill Springs, 8 m. SE Mormon Lake, 7,300 ft., 1 (MVZ). Greenlee Co.: Rose Peak, 8,700 ft., 1 (MVZ).

#### *Sorex nanus* Merriam

*Altitudinal range.*—7,000-9,000 ft. (?).

*Distribution.*—Only 15 specimens of the dwarf shrew have been reported in the literature: one from Montana, six from Colorado, two

from Wyoming, one from Utah, three from New Mexico, and two from Arizona (Clothier, 1957; Findley and Poorbaugh, 1957). The first Arizona specimen, reported by Schellbach (1948), was captured by a fence foreman of the National Park Service as it was running along a log, nine miles east of Swamp Point, on the north rim of the Grand Canyon (Fig. 3). Seven years later, in 1944, a second specimen was found dead in a Grand Canyon lodge, apparently having died there during the winter. This locality is within ten miles of the Swamp Point locality (Hoffmeister, 1955). The other 13 specimens also come from high elevations (Clothier, 1957).

*Records of occurrence.*—Total, 2: Coconino Co.: 9 m. E. Swamp Point, N. Rim Grand Canyon, 7,938 ft., 1 (Grand Canyon Natl. Pk.); Kaibab Lodge, VT Ranch, 1 (UI).

***Sorex palustris navigator* (Baird)**

*Altitudinal range.*—about 8,000-10,000 ft.

*Distribution.*—Water shrews in Arizona are known only from the White Mountains and the Blue Range (Fig. 3). They may also occur in the Rim country, the San Francisco Mountains, the Grand Canyon, and the Kaibab.

Conaway (1952) trapped *S. p. navigator* most commonly along mountain stream banks covered by stones and tree roots. Two of the

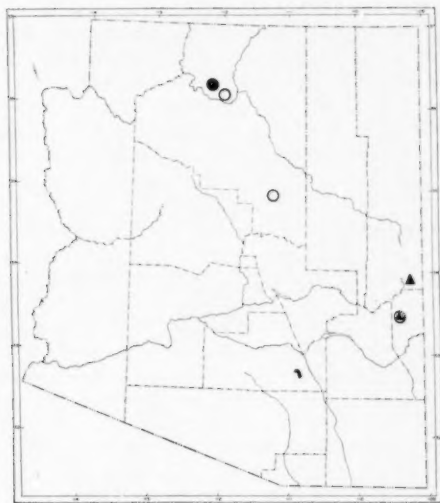


Fig. 3.—Distribution of *Sorex merriami leucogenys* (circles), *S. nanus* (dots), and *S. palustris navigator* (triangles) in Arizona.

three Arizona specimens are from high mountain streams; the third is from a cienega, or marsh. The University of Arizona specimen was caught in a museum special trap, set under a log in a beaver dam in spruce-fir country. Siegler's comments (1956) are noteworthy here. Intensive trapping in beaver lodges at the higher elevations may yield additional specimens of this shrew.

*Records of occurrence.*—Total, 3: Apache Co.: White River, Horseshoe Cienega, 8,300 ft., 1 (BS); Little Colorado River, Sheep Crossing, 9,500 ft., 1 (UA). Greenlee Co.: Prio Plateau, S. end Blue Range, 9,000 ft., 1 (BS).

***Notiosorex crawfordi crawfordi* (Coues)**

*Altitudinal range.*—100-7,000 feet.

*Distribution.*—The gray shrew was not known to occur in Arizona until 1931 when Blossom secured one in the Chiricahua Mountains (1933); there are now 27 state records (Fig. 4). Nine of these come from owl pellets: the six Dragoon Mountains specimens, represented by four skulls and eleven mandibles, five right and six left, recovered from about 100 long-eared owl pellets collected in scattered localities at the edge of the oaks; the Pinal County specimen, represented by one skull and a left mandible, recovered from about 50 barn owl pellets collected in desert shrub habitat (Fig. 5) at 4,200 feet (mesquites, *Prosopis*; palo-verde, *Cercidium*; acacias; yuccas; agaves; and a few *Juniperus*); the San Xavier specimen, represented by the

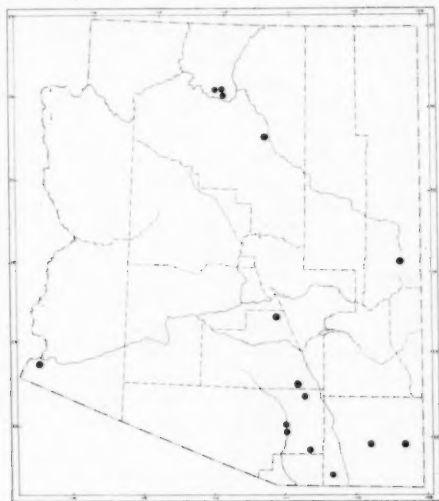


Fig. 4.—Distribution of *Notiosorex crawfordi crawfordi* in Arizona.





Fig. 5.—About five miles southwest of Oracle, Pinal County, 4,200 feet, in the northern foothills of the Santa Catalina Mountains. One *Notiosorex* was recovered from barn owl pellets collected in the shaft at the lower right. Mesquites, opuntias, agaves, grasses, and a juniper are seen in this view.

right upper tooth row and the two mandibles, recovered from one horned owl pellet collected in a mesquite bosque of the Santa Cruz River at 2,500 feet; and the 55 mile specimen, represented by the skull and the two mandibles, recovered from three horned owl pellets collected in a side-gully of the Santa Cruz River among cottonwoods (*Populus Fremontii*) and sycamores (*Platanus Wrightii*), with creosote-bush (*Larrea tridentata*) on the flats adjoining the gully (Fig. 6).

Other arid *Notiosorex* localities in Arizona are: Bright Angel trail, 2,500 feet, in the Lower Sonoran life-zone; Hermit trail, 6,000 feet, in pinyon-juniper country (Lowe, personal communication); Black Falls, 5,500 feet, in northern desert sagebrush; Huachuca Mountains, in agave growth; Santa Rita Mountains; and Yuma, in creosote-bush and salt-bush (*Atriplex*).

Four Arizona specimens, however, come from yellow pine country in four isolated areas: the Desert View specimen, elevation about 7,000 feet; the Springerville specimen, elevation about 6,700 feet; the Chiricahua specimen, elevation 6,500 feet; and the Catalina specimen, elevation 6,000 feet. The Chiricahua *Notiosorex* was taken some 200 feet from permanent water. The Catalina specimen was taken among boulders in a museum special trap (Fig. 7). The Superior, Pinal County, gray shrew was trapped in a rocky area 150 feet from a permanent spring, but in jojoba (*Simmondsia*) habitat at 3,200 feet (Figs. 8 and 9). Cunningham's suggestion with regard to the distribution of the gray shrew in California may apply to Arizona as well:



Fig. 6.—Creosote-bush (*Larrea tridentata*) flats. *Notiosorex* has been trapped in creosote-bush and salt-bush habitat near Yuma, and two gray shrews have been recovered from owl pellets collected in the *Larrea*-bordered Santa Cruz River bottoms south of Tucson.



Fig. 7.—Bear Canyon, Santa Catalina Mountains, Pima County, 6,000 feet. The trees are ponderosa pine; the small tree in the left foreground is silverleaf oak (*Quercus hypoleucoides*); and the grass is longtongue muhly (*Muhlenbergia longiligula*). J. A. Munro trapped a *Notiosorex* among boulders in this locality.

"... it seems advisable to ... regard *Notiosorex* as tolerant of but not necessarily characteristic of desert or Lower Sonoran conditions. ... " (1956).

Dixon (1924) stated that his captive gray shrew preferred meal worms above all other food items. In order of preference, the captive *Notiosorex* of Huey (1936) consumed the following items: moths, beetles, earwigs, crickets, and cockroaches. A gray shrew caught in a California bee-hive was assumed to be eating the larvae of a moth (*Galleria melonella*) that had killed the bees (Willet, 1939). Dixon (1924) mentions other findings of *Notiosorex* in bee-hives. Still other gray shrews have been found in wood-rat (*Neotoma*) nests (Gander, 1929; Davis, 1941); under large, dead agaves (Hoffmeister and Goodpaster, 1954); under cut cornstalks (Dixon, *loc. cit.*); and under rubbish (Hoffmeister and Goodpaster, *loc. cit.*; Cunningham, 1956). Their presence in such areas is attributable to an ample food supply of larval and adult invertebrates.

Patient searching in such localities may result in additional specimens, and supply us with clues towards a fuller understanding of the ecology and life-history of this little-known mammal. Such searching

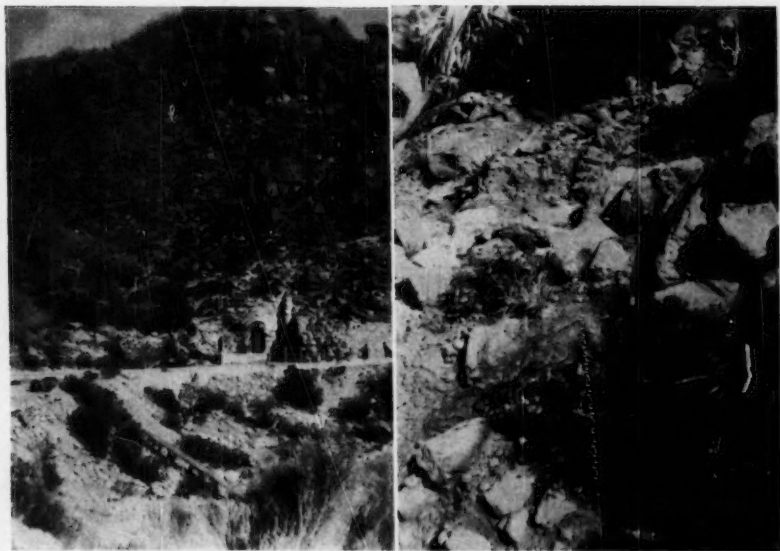


Fig. 8.—About two miles east of Superior, Pinal County, 3,200 feet. One *Notiosorex* was trapped on the hillside, just above the dry wash. The shrubs in the lower right are desert-broom (*Baccharis sarothroides*); those on the hillside are jojoba (*Simmondsia chinensis*) and *Applopappus*.

Fig. 9 (Right).—The collecting locality on the hillside seen in Fig. 8.

by Hoffmeister, *et. al.*, in the Huachuca Mountains resulted in the finding of four *Notiosorex* in an area 60 feet square, and a total of nine records within a three-mile area in one month (1954).

*Records of occurrence.*—Total, 27: Coconino Co.: Hermit Trail, above Hermit Basin, 6,000 ft., 1 (Grand Canyon Natl. Pk.); near bottom Bright Angel trail, Grand Canyon, 2,500 ft., 1 (BS); Desert View Checking Station, S. rim Grand Canyon, 1 (Grand Canyon Natl. Pk.); 10 m. SW Black Falls Indian Ruins, 5,500 ft., 1 (BS). Apache Co.: 1 m. N. Springerville, 1 (UM). Cochise Co.: Pinery Canyon, W. slope, Chiricahua Mts., 6,500 ft., 1 (UM); Dragoon Mts., 6 (UA); Huachuca Mts.: mouth of Ramsey Canyon, 3 (UI), mouth of Carr Canyon, 3 (UI), mouth of Miller Canyon, 1 (UI). Pinal Co.: Burney Mines Rd., ca. 5 m. SW Oracle, 1 (UA); 2 m. E. Superior, 3,200 ft., 1 (UA). Pima Co.: Upper Bear Canyon, Santa Catalina Mts., 6,000 ft., 1 (J. A. Munro); 1 m. SE San Xavier Mission, 2,500 ft., 1 (UA); by the 55 m. post along the Tucson-Nogales Hwy. (55 m. N border), 1 (UA); Santa Rita Exp. Range Hdqs., Santa Rita Mts., 1 (UA). Yuma Co.: Yuma, 2 (BS). In addition, this specimen is herein reported for the first time: 15 m. S Nogales, Les Wooddell Ranch, Sonora, Mexico, 1 (UA). Wt. 3.3 g.

#### SUMMARY

Soricidae in Arizona are represented by five species: *Sorex vagrans monticola*, *S. merriami leucogenys*, *S. nanus*, *S. palustris navigator*, and *Notiosorex crawfordi crawfordi*. The known altitudinal range, geographical distribution, ecological distribution, and records of occurrence are given for each species. It is suggested that *S. m. leucogenys* occurs sympatrically with *S. v. monticola* over a greater part of the range of *monticola* than is presently known, the area of occurrence being higher and cooler elevations. The two state records of *S. nanus* are from high elevations. *S. p. navigator* is known only from the White Mountains and the Blue Range. *Notiosorex* in Arizona is not confined to low deserts; it ranges from sagebrush growth through desert shrub and oaks into yellow pine.

The absence of shrews in certain parts of the state is due to lack of trapping or trapping technique. Collecting localities are suggested for *S. palustris* and *Notiosorex* with the hope that they will aid in uncovering additional specimens.

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# An Ecological Study of a Man-Made Island<sup>1</sup>

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During the summer of 1932, the West Neebish channel of the St. Mary's River was dredged. River-bottom material was drawn up by suction and deposited on a sand bar. The five-acre area of this material, extending above the water level, was named Ecology Island. Conditions were almost ideal for a study of plant establishment and succession on an initially bare area. The study was begun in 1932 and continued until the present.

The purpose of this study has been to record the establishment and succession of plant life on the island, as well as to examine some of the factors governing plant establishment and succession. Special attention was given to the tree species appearing on the island.

Ecology Island is located in the West Neebish channel of the St. Mary's River about  $\frac{1}{2}$  mile northeast of the mouth of the Charlotte River. The location is at the eastern end of the Upper Peninsula of Michigan at  $84^{\circ} 12' W.$  longitude,  $46^{\circ} 19' N.$  latitude.

The climate of Ecology Island is cool and subhumid. Records from the U. S. Weather Bureau Station at Sault Ste. Marie, 17 miles northwest of the island, show an average annual temperature for the period 1932-1954 of  $40.2^{\circ} F.$  and an average temperature for July of  $64.5^{\circ} F.$  Annual precipitation averaged 31.04 inches and exceeded 2 inches for all months of the growing season. Relative humidity seldom drops below 60 percent and winds are moderate, averaging 8.8 miles per hour from the northwest. Solar radiation for the period of April to October 1932-1954 was 44.5 percent of the possible, and seldom exceeded 70 percent for any month. The growing season averaged 128 days between May 17 and September 22. Snow cover extends from November through March.

The general appearance of the island, as seen from the St. Mary's River, is shown in Fig. 1.

The original transect established in 1933 was 200 feet long and 3.3 feet wide. It proceeded  $N 30^{\circ} E$  from the 0 Station, at no time

<sup>1</sup> Journal Article No. 2177 from the Michigan Agricultural Exp. Sta.



Fig. 1.—View of Ecology Island from the west.

being more than 60 feet inland and not crossing the 4-foot contour. In 1936, due to the heavy cover that had developed, the transect was reduced in width to two 1-inch strips, except for arborescent species. A second transect was also established in 1936; it was 528 feet long and 6.6 feet wide. It also began at the 0 Station but proceeded N 83° E and traversed the island at the 10-foot contour. All arborescent species were tallied by height.

By 1941, rising water levels in the St. Mary's River had greatly reduced the length of the original transect, and it was abandoned. The record of herbaceous species was continued using a 1-inch wide strip along the north boundary of the new transect. Rising water

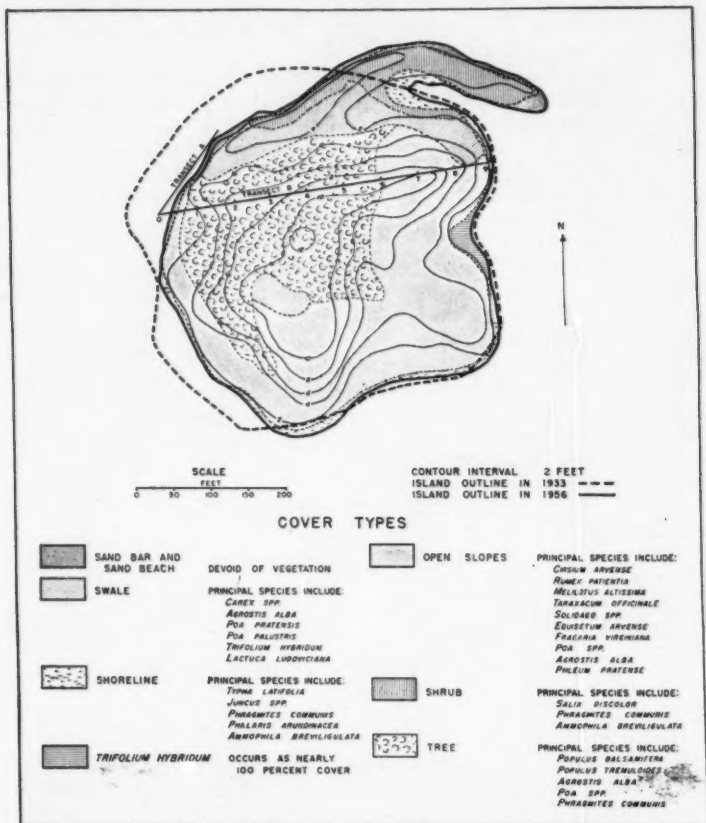


Fig. 2.—Map of Ecology Island.

TABLE I.—Summary of soil data for nine stations along Transect B across Ecology Island

Station No.	Soil Depth Inches	Mechanical Analysis			Organic Matter Percent	Soil Reaction pH	Free CaCO <sub>3</sub> *	Colorimetric Tests							Moisture Equiv.
		Sand	Percent					Ca	P	K	Mg	Cl	SO <sub>4</sub>		
			Silt	Clay											
1	1	88	9	3	1.30	7.7	1	150	86	70	0.2	50	20-	4.83	
1	6	93	3	4	1.23	7.9	2	200	84	66	4.5	30	20-	7.04	
2	1	78	19	3	1.49	7.6	2	200	87	64	3.4	30	20-	16.73	
2	6	58	38	4	0.26	7.5	2	200	86	66	4.5	30	20-	10.14	
3	1	72	25	3	4.58	7.8	2	200	84	70	4.5	30	20-	—	
3	6	28	59	15	—	7.7	2	200	88	76	4.5	30	20-	—	
4	1	44	46	10	1.55	7.4	2	200	86	73	3.4	50	20-	—	
4	6	16	66	18	1.19	7.9	2	200	89	66	4.5	30	20-	—	
5	1	52	40	8	2.46	8.0	2	200	88	58	3.4	30	20-	37.29	
5	6	20	52	18	0.93	8.1	2	200	87	64	3.4	30	20-	30.42	
6	1	66	39	5	2.02	7.5	2	200	84	71	4.5	30	20-	—	
6	6	6	76	18	0.40	7.9	2	200	87	68	3.4	30	20-	—	
7	1	40	50	10	—	7.7	2	200	86	64	3.4	30	20-	—	
7	6	12	67	21	2.23	7.7	2	200	89	61	4.5	30	20-	—	
8	1	48	44	8	4.45	7.3	2	200	85	77	3.4	30	20-	47.85	
8	6	4	74	22	0.32	7.7	2	200	84	73	4.5	30	20-	36.21	
9	1	98	0	2	2.98	7.4	0	60	86	80	1.2	40	20-	9.60	
9	6	96	2	2	0.89	7.5	0	60	88	80	1.2	50	20-	1.74	
60	8	72	20	0.45	7.9	7.9	2	200	88	69	4.5	30	20-	34.59	

\* 0 is weak or no reaction to 10 percent HCL

1 is medium reaction to 10 percent HCL

2 is strong reaction to 10 percent HCL

levels and erosion during the period of 1941 and 1954 reduced the overall length of the transect to 425 feet.

The original shoreline as well as the present contour lines and cover type boundaries are shown in Fig. 2.

The soil sampling technique consisted of taking 5 samples in 1954 at each of 9 uniformly spaced stations along the transect. These samples were taken at 1-inch and 6-inch depths at each station. They were air dried, ground, passed through 60-mesh screen, and then mixed according to their respective location and depth. In addition, one sample was taken at the 5-foot depth to compare with those taken at the 6-inch depth. Ocular examination was made of a trench, 2 feet deep and 10 feet long.

Soil texture determinations were made using the hydrometer method. The organic matter was obtained by using a carbon train to determine total percentage of  $\text{CO}_2$  with a conversion factor of 0.471. The pH determinations were made with a Beckman pH meter. Colorimetric tests were made using standard reagents and standard procedures. Moisture equivalent determinations were made using a centrifuge at 24,500 rpm for 30 minutes.

For purposes of soil description, an identification of parent material is useful. According to Jenny (1941), parent material is that material which at zero time, *in situ*, has not been acted upon by the factors of soil formation. In this sense, then, the effluent river-bottom material became the parent material of Ecology Island. The available plant nutrients, the rather high pH, the moderately high water-holding capacity and the texture of the parent material indicate a fertile medium for plant life.

The results of the soil analyses are summarized in Table I. The soil, or solum, may be considered extremely young. At present it consists only of a very thin layer of organic matter resting upon and mixed with wind-blown sand. The slight tendency for the pH at the 6-inch depth to be higher than that at the 1-inch depth is probably a reflection of additions of sand and organic matter, rather than a reflection of base leaching. The seemingly large differences in percent of organic matter at the 1-inch as compared to the 6-inch depth probably reflects the inclusion of plant roots in the surface soil sample. Under prevailing climatic conditions, such high values in the surface soil are hardly to be expected within 20 years after establishment of the island. Ocular inspection of the holes bored for samples and of the trench revealed a definite structural difference between the 1-inch and 6-inch depths. From 0 to  $\frac{1}{4}$ -inch, structure is crumb to granular; from  $\frac{1}{4}$  to 1-inch, structure is moderately blocky. Weak blocky structure was observed from 1 to 3 inches, coinciding approximately with the zone of most intense root penetration; at 6 inches there was no structure.

It should be noted that conditions at Station 9 vary considerably from the other stations. Station 9 is located at the outermost edge of the river-bottom deposition. Although texture is represented as

nearly 100 percent sand at the 1- and 6-inch depths, pebble to softball size pieces of river-bottom material occur randomly down to 8-inches below the present water level. The sand down to water level is coated with black organic matter, a reflection of past changes in water level. Soil conditions at this station can best be described as dynamic and subject to rapid change.

Attention is drawn to the striking increase in the percent of sand at the 1-inch depth at Stations 3 to 8. The largest percent of the sand is concentrated in the upper fraction of an inch, which is practically all sand mixed with recently deposited organic matter. It represents the deposition of wind-blown sand from the windward shore. Its effect on the rate of infiltration should be beneficial.

Stations 1 and 2 represent the combined influence of wind- and water-borne sand being deposited on the outermost edge of the river-bottom material making up the island. The continual increase in the percent of sand on the surface will result in a continual decrease in water holding capacity. The quality of the surface layer as a seedbed should therefore deteriorate.

The absence of organic matter in the surface layers of soil and the fine texture have tended to make this soil very subject to frost heaving, and this has probably had some influence on successional trends on the island. Frost heaving of seedlings may have prevented some species from becoming established.

A comparison of the cover types and the elevations reveals the dominant role played by elevation above ground water level in the differentiation of cover types (Fig. 2). The shoreline type occurs well within the 2-foot contour interval; the *Trifolium hybridum* colony has its farthest extension at or below the 2-foot contour interval; the swale type predominates between 1 and 3 feet; the open slope type predominates above 3 feet.

Slope also plays a relatively significant role in the ecology of the island. The occurrence of the swale type at approximately the 10-foot contour interval is a result of a marked depression completely enclosed by higher elevations. The effect of slope upon wind-blown sand deposition is best illustrated at Station 6 as compared to Stations 5 and 7. Station 6 is located on the lower portion of a short slope, which obstructs the smooth flow of wind over the island. Station 5 is located on the level approach to the slope, while Station 7 occupies the top of the slope. The percent of sand at the 1-inch depth for Stations 5, 6, and 7 respectively is 52, 66, and 40.

Of major ecological importance are the activities of deer and beaver, particularly the latter. The beaver are responsible in large measure for the rapid increase in the number of aspen and balsam poplar stems per acre, as well as for the areal extension of these species. Sample milacre plots taken throughout the tree cover type revealed an average of 4.7 stems per plot, with a range of 0 to 23. Invariably the plots with a large number of stems had one or more stumps of these species which had been cut by beavers. Aspen and balsam

poplar are propagated mainly by root suckers. Suckering from the roots is greatly stimulated by cutting of the stem. Earlier work in this area (Day, 1944) showed that most of the stems present are root suckers from a few seedlings established soon after the formation of the island. Deer browsing was observed on approximately 30 percent of the stems within the plots, but was confined to the smaller stems, and probably did not greatly affect the rate of suckering.

Wind has been a major factor in the invasion of this bare island by plants. A seed source for practically all species now represented on the island lies directly west on the mainland. Prevailing north-west winds undoubtedly account for the relatively rapid invasion of the island by many species despite the water barrier of a mile or more. Spring and summer storms frequently blow from southerly directions where a seed source is available nearby on Sand Island. It should be noted that the earliest invaders were extremely light-seeded species or had adaptations for air-borne seed.

Wind has also been responsible for the distribution of sand over the surface of the island (see Table I). It will be noticed that the percent of sand in the top 1-inch diminishes gradually from west to east along the transect. The action of the wind has been augmented by the direction of the river current, which flows from north to south. Wave action piles sand up on the beach, and wind action carries it farther across the island.

Since the parent material of Ecology Island is a highly calcareous silt loam, the climax vegetation within this region is almost certainly northern hardwoods. More specifically, the climax vegetation would be the Sugar Maple—Beech—Yellow Birch type as defined by the Society of American Foresters (1954).

At present, several stages in the succession to the climax vegetation are found on the island. They are illustrated by the shoreline, swale, open slope and tree types. The very occurrence of these stages represents a more stable condition as compared to the early history of the island when migration and ecesis were the dominant successional processes. By 1941, the island was almost completely occupied by vegetation and competition began to emerge as the dominant successional process, although migration and ecesis were still active.

A listing of the species found on the transects at the time of the various examinations as well as a check list for the entire island appears at the end of this article.

Since data from transect A were considered useful mainly as a record of pioneer species, only data from transect B were used in studying density changes. Transect B was divided into 1-foot subplots. When tallies were made in 1946 and 1954, three observations were recorded for each subplot. These were: 1.—species occurring; 2.—relative abundance of each species; 3.—relative density of the entire subplot. The last two observations were determined ocularly. Relative abundance was recorded as (3) fully occupied, (2) partially occupied, but not sparse, and (1) sparse. A summary of the data



for relative density is shown in Table II. The percentages are based on 422 subplots, since 28 subplots on the west side of the island were lost between 1946 and 1954 due to inundation and erosion.

The most significant shift in total relative density is the 13 percent increase in fully occupied subplots with a corresponding decrease in the medium density group in 1954 as compared to 1946. Of more importance than the shift in total relative density is the shift in the distribution of relative density among the subplots of the east and west portions of the transect. These results, for the 422 subplots involved, are summarized in Table III.

TABLE II.—Distribution of subplots along Transect B by relative density classes of vegetation

Year of Observation	3	Relative Density Class		Total
		2	1	
		Percent		
1946	49	31	20	100
1954	62	17	21	100

TABLE III.—Distribution of subplots along the east and west portions of Transect B by relative density classes of vegetation

Year of Observation	3		Relative Density Class 2 and 1		Total	
	0-4	4-9	Stations		0-4	4-9
			0-4	4-9		
			Percent			
1946	50	49	50	51	100	100
1954	12	97	88	3	100	100

The summary shows a decrease in fully stocked plots from 50 to 12 percent to the windward of Station 4 and an increase in fully stocked plots from 49 to 97 percent on the west side of Station 4. These changes are probably due to the effects of sand deposition primarily to the windward of Station 4. The more rapid rate of water loss and the much lower water holding capacity occasioned by the increased percentage of sand would lead to a drier site. This effect would be augmented by the more southerly exposure of Stations 0 to 4, as well as by the more direct wind movement over this portion of the island. The diminishing occurrence of *Phragmites communis*, a moist site species, over this portion of the island supports this explanation.

Changes in composition of herbaceous vegetation were evaluated in terms of species occurrence and abundance. Table IV shows the actual number of subplots, by date of examination, in which each species occurs and its relative abundance index, for Transect B. The relative abundance index was derived as follows: The most abundant

TABLE IV.—Occurrence and relative abundance of herbaceous species along Transect B on Ecology Island

Grasses and Grass-like Species	Date of observation	No. of subplots	Relative Abundance index
<i>Agrostis alba</i>	1941	8	2.75
	1946	7	2.40
	1954	63	2.27
<i>Calamagrostis canadensis</i>	1941	16	1.31
	1946	19	1.47
	1954	0	none
<i>Elymus virginicus</i>	1941	0	none
	1946	18	2.22
	1954	1	3.00
<i>Equisetum arvense</i>	1941	141	1.62
	1946	337	1.18
	1954	306	1.46
<i>Hordeum jubatum</i>	1941	100	1.80
	1946	13	2.85
	1954	0	none
<i>Phleum pratense</i>	1941	55	2.00
	1946	79	2.01
	1954	53	3.11
<i>Phragmites communis</i>	1941	58	1.60
	1946	96	1.64
	1954	36	2.33
<i>Poa spp.</i>	1941	132	2.17
	1946	170	2.16
	1954	242	2.25
Herbaceous Species			
<i>Aster spp.</i>	1941	2	3.00
	1946	14	1.64
	1954	3	3.33
<i>Cirsium arvense</i>	1941	90	1.77
	1946	74	2.17
	1954	13	2.78
<i>Fragaria virginiana</i>	1941	8	2.13
	1946	62	2.03
	1954	121	2.90
<i>Erigeron spp.</i>	1941	94	1.91
	1946	0	none
	1954	0	none
<i>Melilotus altissima</i>	1941	0	none
	1946	4	3.75
	1954	86	1.05
<i>Polygonum Convolvulus</i>	1941	149	2.62
	1946	0	none
	1954	0	none
<i>Solidago spp.</i>	1941	6	1.00
	1946	60	2.25
	1954	52	2.38
<i>Taraxacum officinale</i>	1941	1	1.00
	1946	3	4.00
	1954	53	3.83
<i>Trifolium hybridum</i>	1941	0	none
	1946	23	1.70
	1954	63	2.03

species occurring in a subplot was listed first (or 1), the second most abundant second (or 2) and so forth. These values were added for all the subplots for each species and divided by the number of subplots in which each species occurred. For example, if a species occurred in 10 subplots as 1, 1, 1, 2, 3, 1, 1, 2, 1, 2—it would have a relative abundance index of  $15/10$  or 1.5. Thus, the lower the index value, the greater the relative abundance.

The relationships shown in Table IV provide a clear picture of past changes in composition within the successional stages. They also provide a key for predictions of future changes. In nearly every instance, a decrease in number of subplots occupied is associated with a corresponding decrease in relative abundance (increase in index value). This relationship is particularly conspicuous for *Phleum pratense*, *Phragmites communis*, *Aster spp.*, and *Cirsium arvense*. These species probably will be among the first to disappear from that part of the transect occupied by the tree and open slope types, while *Phleum pratense* and *Phragmites communis* will persist in the shoreline or swale types.

Another group, characterized by *Agrostis alba* and *Melilotus altissima*, is increasing both in abundance and occurrence. Just what types they will occupy remains to be seen, although *Agrostis alba* has demonstrated its ability to compete successfully in the open slope and tree types, while *Melilotus altissima* appears able to compete successfully in the swale and open slope types.

A third group of species, exemplified by *Poa spp.*, *Equisetum arvense* and *Trifolium hybridum*, appears to maintain about the same relative abundance index whether the number of subplots occupied increases or decreases. *Poa spp.*, appear to be retreating on the driest sites, or from the windward shore to Station 3, while increasing over the remaining portion of the transect. *Trifolium hybridum*, a typical



Fig. 3.—View of tree cover type near center of Island.

wet site species, has been able to compete successfully within the shoreline, swale and lower portions of the open slope types. Clover has a well-developed tap root which probably is primarily responsible for its success on the drier, windward side of the island.

The most important tree species on the island are *Populus tremuloides* and *Populus balsamifera*; *Salix spp.* is restricted primarily to shoreline sites (Fig. 3). It appears that aspen and balsam poplar will soon dominate the area now occupied by the swale, open slope

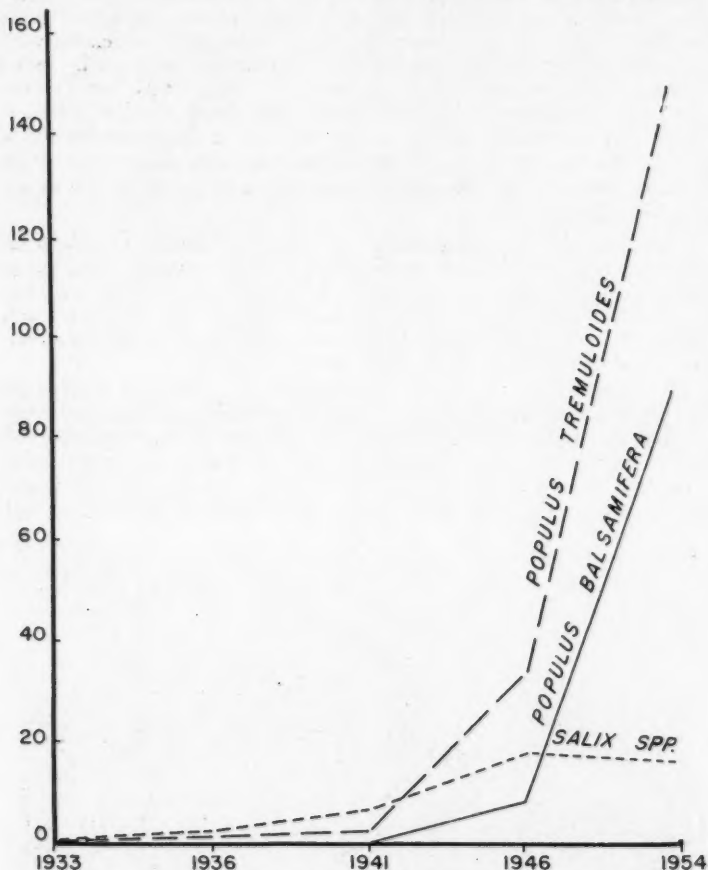


Fig. 4.—The occurrence of tree species along Transect B on Ecology Island, 1933 to 1954.

and tree types, with balsam poplar favoring the more moist sites. Although site requirements for best aspen growth are restrictive, this species is able to occupy all but the wettest and driest sites. These species have already demonstrated their ability to compete successfully with all species on the island, with the possible exception of *Melilotus altissima*. The rapid initial growth of the suckers prevents their being overtopped by any other species now on the island. The number of stems per acre and the total area occupied is presently increasing at a rapid rate as shown by Fig. 4. Extension of the type is due in large part to the beaver cuttings resulting in the continual production of root suckers, and preventing stabilization of the type boundary. At the present time, the beavers have cut all stems of these species on the island that are over two and one-half inches in diameter.

#### SUMMARY

Ecology Island was created in the summer of 1932 as the result of a dredging operation. Highly calcareous, silt loam river-bottom material was deposited on a sand bar. The area covered by this material above the water level was approximately five acres and at its highest point was originally 14 feet above the water level. Transect A was established in 1933 to sample herbaceous vegetation. It was abandoned in 1941 as a result of rising water level. Transect B was established in 1936 to sample arborescent species. After Transect A was abandoned, sampling of herbaceous vegetation was continued on Transect B.

Successional changes on the island have been rapid by ordinary standards. Factors which appear to account for these changes are as follows:

1. Significant alterations have already occurred on the physical site itself. The ground water level has risen nearly two feet as a result of a rise in the water level of the river. Wave and wind action have combined to deposit appreciable amounts of sand over the surface on the windward side of the island, resulting in continually more xeric surface conditions.
2. The fertile river-bottom material, combined with the temperate climate, can sustain very advanced forms of plant life. Although the climax species for this region (Sugar Maple-Beech-Yellow Birch) have not yet appeared, species preceding the climax, aspen and balsam poplar, are well represented.
3. A good seed source together with the prevailing winds combined to favor rapid invasion by many species.
4. By 1941, the island was nearly 100 percent occupied. Competition between species became intense early in the history of the island. Several early invaders have already disappeared, while site boundaries for nearly all remaining species are very dynamic.

Future successional changes are predicted by considering past changes and the factors favoring one species over another. With few exceptions the dominant vegetation on the island consists of perennials. Most of the annuals have been or are being replaced. Among the perennials, *Agrostis alba*, *Poa spp.*, *Equisetum arvense*, *Fragaria virginiana*, *Trifolium hybridum*, *Populus tremuloides* and *Populus balsamifera* have emerged as the more successful competitors to date. *Phragmites communis* continues to be an important species, but is successful only on the wet sites. *Melilotus altissima*, a biennial, must be included in the list of successful competitors.

In direct competition, *Melilotus altissima* is more successful than the grasses, *Equisetum arvense* and *Fragaria virginiana*. Its height, tap root system and lime requirement probably account for its success. *Trifolium hybridum* is most successful on wet sites. *Populus balsamifera* and *Populus tremuloides* dominate the site they now occupy. They have not as yet come into direct competition with *Melilotus altissima*. When they do, however, it is quite likely that they will dominate this species. They are favored by their rapid initial height growth, their height at maturity, and in the case of *Populus tremuloides* by its less exacting site requirements.

#### LIST OF PLANT SPECIES ARRANGED BY OCCURRENCE IN TRANSECT AND YEAR

##### TRANSECT A

###### SPECIES FOUND IN 1936

- |   |                                     |
|---|-------------------------------------|
| 1. <i>Equisetum arvense</i> L.                        | 7. <i>Typha latifolia</i> L.        |
| 2. <i>Carex spp.</i>                                  | 8. <i>Phragmites communis</i> Trin. |
| 3. <i>Sagittaria latifolia</i> Willd.                 | 9. <i>Chenopodium album</i> L.      |
| 4. <i>Juncus spp.</i>                                 | 10. <i>Polygonum convolvulus</i> L. |
| 5. <i>Lycopus americanus</i> Muhl.                    | 11. <i>Rumex Patientia</i> L.       |
| 6. <i>Calamagrostis canadensis</i><br>(Michx.) Beauv. | 12. <i>Elymus virginicus</i> L.     |
|   | 13. <i>Solidago canadensis</i> L.   |

##### TRANSECT A

###### SPECIES FOUND IN 1940

- |   |                                     |
|---|-------------------------------------|
| 1. <i>Equisetum arvense</i> L.                        | 7. <i>Typha latifolia</i> L.        |
| 2. <i>Carex spp.</i>                                  | 8. <i>Phragmites communis</i> Trin. |
| 3. <i>Sagittaria latifolia</i> Willd.                 | 9. <i>Chenopodium album</i> L.      |
| 4. <i>Juncus spp.</i>                                 | 10. <i>Polygonum convolvulus</i> L. |
| 5. —missing <sup>1</sup> —                            | 11. <i>Rumex Patientia</i> L.       |
| 6. <i>Calamagrostis canadensis</i><br>(Michx.) Beauv. | 12. <i>Elymus virginicus</i> L.     |
|   | 13. <i>Solidago canadensis</i> L.   |

###### SPECIES FOUND IN 1940, BUT NOT IN 1936

- |   |                                       |
|---|---------------------------------------|
| 14. <i>Agrostis alba</i> L.             | 19. <i>Poa pratensis</i> L.           |
| 15. <i>Phleum pratense</i> L.           | 20. <i>Erigeron canadensis</i> Gray.  |
| 16. <i>Monarda didyma</i> L.            | 21. <i>Polygonum spp.</i>             |
| 17. <i>Eleocharis spp.</i>              | 22. <i>Cirsium arvense</i> (L.) Scop. |
| 18. <i>Ranunculus pennsylvanicus</i> L. |                                       |



## TRANSECT B

## SPECIES FOUND IN 1941

- |  |   |
|--|---|
| 1. <i>Equisetum arvense</i> L.                     | 14. <i>Polygonum Convolvulus</i> L.           |
| 2. <i>Carex</i> spp.                               | 15. <i>Erigeron canadensis</i> Gray           |
| 3. <i>Calamagrostis canadensis</i> (Michx.) Beauv. | 16. <i>Cirsium arvense</i> (L.) Scop.         |
| 4. <i>Typha latifolia</i> L.                       | 17. <i>Oenothera biennis</i> L.               |
| 5. <i>Phragmites communis</i> Trin.                | 18. <i>Solidago canadensis</i> L.             |
| 6. <i>Rumex Patientia</i> L.                       | 19. <i>Hordeum jubatum</i> L.                 |
| 7. <i>Elymus virginicus</i> L.                     | 20. <i>Aster</i> spp.                         |
| 8. <i>Agrostis alba</i> L.                         | 21. <i>Fragaria virginiana</i> Duchesne       |
| 9. <i>Phleum pratense</i> L.                       | 22. <i>Taraxacum officinale</i> Weber         |
| 10. <i>Ranunculus pennsylvanicus</i> L.            | 23. <i>Achillea Millefolium</i> L.            |
| 11. <i>Poa pratensis</i> L.                        | 24. <i>Eupatorium perfoliatum</i> L.          |
| 12. <i>Poa palustris</i> L.                        | 25. <i>Gerardia paupercula</i> (Gray) Britton |
| 13. <i>Poa compressa</i> L.                        |   |

## TRANSECT B

## SPECIES FOUND IN 1946

- |  |  |
|--|--|
| 1. <i>Equisetum arvense</i> L.                     | 14. —missing—  |
| 2. —missing <sup>2</sup> —                         | 15. —missing—  |
| 3. <i>Calamagrostis canadensis</i> (Michx.) Beauv. | 16. <i>Cirsium arvense</i> (L.) Scop.  |
| 4. —missing—                                       | 17. <i>Oenothera biennis</i> L.  |
| 5. <i>Phragmites communis</i> Trin.                | 18. <i>Solidago canadensis</i> L.  |
| 6. <i>Rumex Patientia</i> L.                       | 19. <i>Hordeum jubatum</i> L.  |
| 7. <i>Elymus virginicus</i> L.                     | 20. <i>Aster</i> spp. (identified as <i>A. simplex</i> Willd.; <i>tradiflorus</i> L.; and <i>dumosus</i> L.) |
| 8. <i>Agrostis alba</i> L.                         | 21. <i>Fragaria virginiana</i> Duchesne  |
| 9. <i>Phleum pratense</i> L.                       | 22. <i>Taraxacum officinale</i> Weber  |
| 10. —missing—                                      | 23. —missing—  |
| 11. <i>Poa pratensis</i> L.                        | 24. —missing—  |
| 12. <i>Poa palustris</i> L.                        | 25. —missing—  |
| 13. —missing—                                      |  |

## SPECIES FOUND IN 1946, BUT NOT IN 1941

- |   |  |
|---|--|
| 26. <i>Galium trifidum</i> L.                             | 30. <i>Epilobium angustifolium</i> L.    |
| 27. <i>Solidago gigantea</i> var. <i>leiophylla</i> Fern. | 31. <i>Ammophila breviligulata</i> Fern. |
| 18. <i>Erigeron philadelphicus</i> L.                     | 32. <i>Melilotus altissima</i> Thuill.   |
| 29. <i>Solidago graminifolia</i> (L.) Salisb.             | 33. <i>Trifolium hybridum</i> L.         |

## TRANSECT B

## SPECIES FOUND IN 1954

- |   |                                       |
|---|---------------------------------------|
| 1. <i>Equisetum arvense</i> L.  | 10. —missing—                         |
| 2. <i>Carex</i> spp. (identified as <i>C. retrorsa</i> Schw.; <i>vulpinoidea</i> Michx.; <i>scoparia</i> Schk.) | 11. —missing—                         |
| 3. —missing <sup>3</sup> —  | 12. <i>Poa palustris</i> L.           |
| 4. —missing—  | 13. <i>Poa compressa</i> L.           |
| 5. <i>Phragmites communis</i> Trin.   | 14. —missing—                         |
| 6. —missing—  | 15. —missing—                         |
| 7. <i>Elymus virginicus</i> L.  | 16. <i>Cirsium arvense</i> (L.) Scop. |
| 8. <i>Agrostis alba</i> L.  | 17. —missing—                         |
| 9. <i>Phleum pratense</i> L.  | 18. <i>Solidago canadensis</i> L.     |
|   | 19. —missing—                         |
|   | 20. <i>Aster</i> spp.                 |

- |   |                                       |
|---|---------------------------------------|
| 21. <i>Fragaria virginiana</i> Duchesne                   | 28. —missing—                         |
| 22. <i>Taraxacum officinale</i> Weber                     | 29. <i>Solidago graminifolia</i> (L.) |
| 23. —missing—   | Salisb.                               |
| 24. —missing—   | 30. <i>Epilobium angustifolium</i> L. |
| 25. —missing—   | 31. —missing—                         |
| 26. <i>Galium trifidum</i> L.                             | 32. <i>Melilotus altissima</i> Thuill |
| 27. <i>Solidago gigantea</i> var. <i>leiophylla</i> Fern. | 33. <i>Trifolium hybridum</i> L.      |

## SPECIES FOUND IN 1954, BUT NOT IN 1941 OR 1946

- |                                      |                                     |
|--------------------------------------|-------------------------------------|
| 34. <i>Lactuca sagittifolia</i> Ell. | 39. <i>Phalaris arundinacea</i> L.  |
| 35. <i>Hieracium aurantiacum</i> L.  | 40. <i>Juncus brachycephalus</i>    |
| 36. <i>Rumex crispus</i> L.          | (Engelm.) Buch.                     |
| 37. <i>Iris versicolor</i> L.        | 41. <i>Juncus canadensis</i> J. Gay |
| 38. <i>Scirpus americanus</i> Pers.  |                                     |

CHECK LIST OF SPECIES FOUND ON THE ENTIRE ISLAND  
1946

## Trees

- |                                      |                                |
|--------------------------------------|--------------------------------|
| 1. <i>Populus balsamifera</i> L.     | 3. <i>Prunus virginiana</i> L. |
| 2. <i>Populus tremuloides</i> Michx. | 4. <i>Salix nigra</i> Marsh.   |

## Shrubs

- |  |                                  |
|--|----------------------------------|
| 1. <i>Amelanchier canadensis</i> (L.)<br>Medic | 2. <i>Salix discolor</i> , Muhl. |
|--|----------------------------------|

## Grass and Grass-like Plants

- |   |                                      |
|---|--------------------------------------|
| 1. <i>Agropyron repens</i> (L.) Beauv.                | 13. <i>Hordeum jubatum</i> L.        |
| 2. <i>Agrostis alba</i> L.                            | 14. <i>Juncus brachycephalus</i>     |
| 3. <i>Agrostis hyemalis</i> (Walt.) BSP               | (Engelm.) Buch.                      |
| 4. <i>Ammophila breviligulata</i> Fern.               | 15. <i>Juncus canadensis</i> J. Gay  |
| 5. <i>Calamagrostis canadensis</i><br>(Michx.) Beauv. | 16. <i>Juncus effusus</i> L.         |
| 6. <i>Carex retrorsa</i> Schw.                        | 17. <i>Phleum pratense</i> L.        |
| 7. <i>Carex scoparia</i> Schk.                        | 18. <i>Phragmites communis</i> Trin. |
| 8. <i>Carex vulpinoidea</i> Michx.                    | 19. <i>Poa compressa</i> L.          |
| 9. <i>Elymus glaucus</i> Buckl.                       | 20. <i>Poa palustris</i> L.          |
| 10. <i>Elymus virginicus</i> L.                       | 21. <i>Poa pratensis</i> L.          |
| 11. <i>Equisetum arvense</i> L.                       | 22. <i>Scirpus americanus</i> Pers.  |
| 12. <i>Glyceria grandis</i> S. Wats.                  |                                      |

## Herbaceous Plants

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|--|--|
| 1. <i>Achillea Millefolium</i> L.                | 11. <i>Chrysanthemum Leucanthemum</i><br>var. <i>pinnatifidum</i> Lecoq. &<br>Lamotte. |
| 2. <i>Anaphalis margaritacea</i><br>(L.) B. & H. | 12. <i>Cirsium arvense</i> (L.) Scop.  |
| 3. <i>Apocynum androsaemifolium</i> L.           | 13. <i>Epilobium angustifolium</i> L.  |
| 4. <i>Asclepias syriaca</i> L.                   | 14. <i>Epilobium palustre</i> L.   |
| 5. <i>Aster dumosus</i> L.                       | 15. <i>Erigeron-ramosus</i> (Walt.) BSP  |
| 6. <i>Aster simplex</i> Willd.                   | 16. <i>Eupatorium perfoliatum</i> L.   |
| 7. <i>Aster tardiflorus</i> L.                   | 17. <i>Fragaria virginiana</i> Duchesne  |
| 8. <i>Aster umbellatus</i> Mill.                 | 18. <i>Galium trifidum</i> L.  |
| 9. <i>Bidens frondosa</i> L.                     |  |
| 10. <i>Chenopodium album</i> L.                  |  |

- |  |  |
|--|--|
| 19. <i>Gerardia paupercula</i> (Gray)<br>Britton | 33. <i>Potentilla monspeliensis</i> L.                       |
| 20. <i>Geum canadense</i> Jacq.                  | 34. <i>Ranunculus pensylvanicus</i> L.                       |
| 21. <i>Hieracium aurantiacum</i> L.              | 35. <i>Rumex crispus</i> L.                                  |
| 22. <i>Hieracium Gronovii</i> L.                 | 36. <i>Rumex Patientia</i> L.                                |
| 23. <i>Lactuca ludoviciana</i> (Nutt.) DC        | 37. <i>Sagittaria cuneata</i> Sheldon                        |
| 24. <i>Lactuca serriola</i> L.                   | 38. <i>Sium cicutaefolium</i> Schrank                        |
| 25. <i>Lycopus americanus</i> Muhl.              | 39. <i>Solidago canadensis</i> L.                            |
| 26. <i>Lysimachia terrestris</i> (L.) BSP        | 40. <i>Solidago gigantea</i> var.<br><i>leiophylla</i> Fern. |
| 27. <i>Melilotus altissima</i> Thuill.           | 41. <i>Solidago nemoralis</i> Ait.                           |
| 28. <i>Mentha canadensis</i> (L.) Briquet.       | 42. <i>Solidago rugosa</i> Mill.                             |
| 29. <i>Mimulus ringens</i> L.                    | 43. <i>Taraxacum officinale</i> Weber                        |
| 30. <i>Oenothera biennis</i> L.                  | 44. <i>Trifolium hybridum</i> L.                             |
| 31. <i>Polygonum Convolvulus</i> L.              | 45. <i>Typha latifolia</i> L.                                |
| 32. <i>Polygonum lapathifolium</i> L.            |  |

<sup>1</sup> The same number has been used for the same species in both 1936 and 1940. "Missing" indicates that the species was present on Transect A in 1936, but not in 1940.

<sup>2</sup> The same number has been used for the same species in 1941, 1946 and 1954. "Missing" indicates that the species was present on Transect B in 1941, but not in 1946.

<sup>3</sup> Species present on Transect B in 1941 or in 1946, but not in 1954.

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## Flight Activities of Two Species of Ants of the Genus *Formica*<sup>1</sup>

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This paper is a description of flight activities of *Formica obscuripes* Forel and *Formica ulkei* Emery which occurred on the Edwin S. George Reserve, Livingston County, Michigan. Although each species has been studied rather extensively, there have been no previously published records of nuptial flights. On the contrary, each has been suspected of having no true flights, or of having flights which are very limited in extent (Weber, 1935 and Holmquist, 1928).

### FORMICA OBSCURIPES Forel

Neal Weber (1935) has reported that *F. obscuripes* in North Dakota probably does not have true nuptial flights. He said that the winged forms simply leave the nest, singly or a few at a time, during the month of June, whenever the temperature is above 60°F., humidity exceeds 50 percent, and the sky is clear. In southern Michigan, *F. obscuripes* has a series of conspicuous and abundant flights.

Fourteen mounds of *F. obscuripes* were found on the Edwin S. George Reserve, all near its south border and all on the slope of high, rather dry fields. Flights were seen from three different colonies (1953, '54, '56), but complete records were kept for the 1956 flight only. This colony was located in an open field, about two-thirds down a slope which faced west. Vegetation near the nest consisted largely of Canada bluegrass (*Poa compressa* L.) with a lesser amount of Kentucky bluegrass (*Poa pratensis* L.), together with cinquefoil (*Potentilla simplex* Michx.) and wild bergamot (*Monarda fistulosa* L.). Circling the nest and half way up its sides was a denser, taller growth of the bluegrasses and timothy (*Phleum pratense* L.). These grasses were used by the winged ants as a starting place for flights. The mound nest was dome-shaped and nearly circular, eight inches high on the uphill side and twelve inches high on the downhill side. The bare thatch top was 20 by 21 inches and the whole mound was 31 by 34 inches across. It was one of the larger mounds, although not the largest.

The first flight of the season was not seen, and perhaps several flights had occurred before observations began on June 16, 1956. Ten flights were watched over a period of fourteen days (four days had

<sup>1</sup> The work was assisted by a grant from the Edwin S. George Reserve scholarship fund. Facilities of the Reserve were made available by Dr. T. H. Hubbel, Acting Director, and Dr. Irving J. Cantrall, Curator of the Reserve.

no flights), and these were all checked from the time that the first winged ants began coming from the nest until the last had flown or retreated (see Table I). An attempt was made to count the number of ants flying each minute, so that a fairly good estimate of the number leaving the nest each day was obtained. Temperature and relative humidity records were kept, but the latter are not given, for they always seemed to be within the range of tolerance.

In *F. obscuripes* there occurred a partial segregation of the sexes. Males flew in the first days; then their numbers diminished as those of females increased. On the first day when flights were observed (June 16), there was a moderate completely male flight. As the weather was unfavorable for the next two days, no flying occurred. June 19 was the big day for male flight; an estimated 4,000 flew. On this day several females came to the surface, and three flew. Next day about a hundred males and a dozen females flew, and on the next the ratio was reversed, for at least 130 females flew, together with about a dozen males. Only five more males were seen to fly on subsequent days, although as late as June 26 several males, apparently unable to fly, were seen. Females had their best flight on June 22, when over 230 flew.

Since all female flights were observed, a fairly accurate estimate of females produced could be made. Six hundred and ninety-five were counted. This was, of course, an undercount since some must have been missed. The count of males cannot be so accurate. An estimated 4,500 flew on the days when flights were watched, but there may have been male flights before observations began.

Both males and females flew from grasses surrounding the mound, not from the mound itself. At times there were as many as 100 males or 85 females on the tips of grass flowers and blades, and these made a conspicuous sight. They flew quickly, with little preliminary fluttering of wings. Females flew as readily as did the males. Most of both sexes flew down hill and westward over the swamp. As flying continued, more winged ants kept coming from the nest. On fine days it seemed that all flew that came out, but when conditions became unfavorable, both males and females would walk down and into nest entrances.

On June 16 there was a typical, moderate male flight. At 6:30 a.m. (EST) (69°F.), males began coming from the nest exits, and within five minutes had begun to climb grasses. At 7:04 a.m. there were 34 males on the grasses, and the first one flew. By 7:30 a.m. (71°F.), four had flown and there were more than 100 black males standing on grass tips or walking about on the grasses. In the next 30 minutes they flew at the rate of two or three a minute, then increased to eight or ten a minute for another ten minutes (74°F.). By this time, few were coming from the nest and the number on grasses had dropped to about 50. Flying slowed to four or five a minute. The last one flew at 8:17 a.m. (74°F.), and others on the grasses made

their way down into the nest as the sky became a bit more overcast.

A typical female flight occurred on June 22. The day was sunny, and at 5:45 a.m. (64°F.) one female was on the mound with the workers. At 6:35 a.m. (66°F.), two began to climb grasses and more were coming from nest entrances. By 7:00 a.m. (70°F.), 34 were standing on plants and the first one flew. The temperature being right, they flew at the rate of two a minute for ten minutes and then at four a minute for 45 minutes (72°-77°F.). During this time they were flying at nearly the same rate as they were coming from the nest, so not more than 38 were counted on grasses at any time. Some flew very quickly after they climbed, but others maneuvered a bit for a good take-off. In doing this, they would open their wings and drop (or fly several inches and drop) from one blade to a lower one or to the ground, and then climb again quickly. The urge to walk upward seemed very great; females walked down only when conditions for flight were unfavorable. By eight o'clock, flight had slackened because fewer were coming from the nest, but it continued at the rate of about one a minute for another 20 minutes (80°F.), then stopped because all on the grass had flown.

During *F. obscuripes* flights, weather conditions fluctuated enough from day to day to give evidence of certain controlling factors. Flights occurred in the morning but varied in the time of beginning and ending. They might begin as early as 5:00 a.m. or as late as 11:35 a.m. and end at any time from 7:50 a.m. to 11:40 a.m. In contrast, the ants reacted rather precisely to temperature changes. They began coming to the surface of the mound as temperatures approached the mid-60's, and climbed grass stems soon after. Flying could begin at 69°F., although few flew at that temperature, and 70° to 71°F. was the usual starting point. Flying reached heights between 72° and 77°F. and ceased altogether beyond 81°F. Three other variables besides temperature were found to influence flight. Any gust of wind

TABLE I.—Flights of *Formica obscuripes*, 1956

Date	First winged ants left nest		First climbed grass	
6-16	69°	6:30	69°	6:35
6-19	62°	7:50	67°	8:30
6-20	68°	6:45	69°	7:00
6-21	68°	5:30	69°	5:45
6-22	64°	5:40	65°	6:00
6-23	68°	5:20	71°	5:45
6-24	66°	5:50	68°	7:10
6-25	67°	8:30	68°	10:10
6-26	63°	7:20	67°	7:45
6-29	64°	7:45	66°	8:15

Temperature in degrees F.; time a.m.



that swayed the grasses would stop flying momentarily, and on June 27, strong winds prevented winged ants from coming out, even though temperatures were favorable. Progressive darkening of the sky, even at such temperatures, caused ants to move down grass-blades and into the nest. The flight on June 23 was stopped completely in this way for a period of an hour and fifteen minutes. All of the females walked down and into the nest, and it looked as if flight was over; then the sun broke through the clouds, and they began climbing and flying again. A uniformly gray sky did not prevent flight, but prolonged it, presumably because the temperatures rose slowly. Wet grasses delayed flying. On June 21, females climbed thoroughly wet grass and then stood for about twenty minutes before flying. As a result great numbers of females were standing on the grasses—as many as 84—because they were coming from the nest faster than they could get dry and fly.

Thus ants began flying at about 70°F., provided they were not wet, the grass was not swaying, and the sky was not darkening. If the sun remained bright and temperature continued to rise, flight was probably stopped when the bare surface of the mound became too hot for ants to come from the nest. On other days, dropping temperature or darkening skies with the threat of rain could stop flights.

On four days no flights occurred. On June 18 and 28, temperatures did not rise above 67°F. and the sky was dull. On June 17, it rained during the morning, and on June 27, heavy winds prevented flight though temperatures were favorable.

It will be noted in Table I that the flight of three ants on one day and of eight ants on another were considered to constitute flights. These were included because typical flight activities occurred each day. On June 25, females came out at 8:30 a.m. (67°F.) although the sky was completely overcast. As the temperature rose a bit, a

TABLE I.—(continued)

	Beginning		Flight Height		End		Numbers which flew	
							Male	Female
6-16	70°	7:04	74°-74°	8:00-8:10	74°	8:17	286	—
6-19	70°	9:11	74°-76°	9:20-9:40	81°	10:00	4000	3
6-20	70°	7:15	73°-74°	8:35-9:00	76°	9:35	88	12
6-21	69°	6:08	75°-76°	7:05-7:25	79°	8:00	12	130
6-22	70°	7:00	72°-77°	7:10-7:55	80°	8:15	4	218
6-23	71°	5:50	76°-74°	7:20-7:35	76°	9:49	—	30
6-24	70°	7:30	73°-75°	7:40-8:00	80°	8:25	1	190
6-25	72°	11:35			73°	11:40	—	3
6-26	71°	8:05	71°-77°	8:05-8:55	78°	9:30	—	101
6-29	70°	8:20			78°	10:05	—	8

Temperature in degrees F.; time a.m.

few would climb grasses, only to go down again as it dropped a degree or two. This kept up all morning until at 11:35 a.m. the sky cleared briefly and three ants succeeded in flying during five minutes of favorable temperature. On June 29, the eight ants which flew were the only ones remaining in the colony. Flight was prolonged on this day because temperature kept fluctuating above and below the critical point. Next day, conditions were just right for flying, but no more winged ants appeared.

It is easy to see how one might gain the impression that winged ants leave the nest singly or a few at a time if one observes the nest under conditions which are not quite right for flight. On June 26, by 9:05 a.m., 86 females had flown and there were no more in sight. Then for the next twenty-five minutes, females kept coming up and flying, one or two at a time, until fifteen more had flown. During this time, there were never more than four in sight at one time. However, when flying conditions are right, *F. obscuripes* in Michigan has typical flights.

*F. obscuripes* also has conspicuous swarming and mating activities. These were not observed until June 4, 1958, when ants from three colonies, instead of flying away, gathered in a little valley-like depression near the nests. (This may have occurred because the sky was uniformly overcast.) The swarm covered an oval 30 yards long by 12 yards wide in an area of Kentucky bluegrass which was in bloom and stood about 15 inches tall. Females lighted on the grass culms while males gathered just above the grass and flew up and down among the grass blades, stopping briefly at one after another until a female was found. A brief struggle would take place and then the female usually stood quietly with the male curled up above her gaster. Sometimes two or three males struggled for a female in a rough-and-tumble which caused them to fall. All mating took place on grass blades and each lasted a minute, or a little more. There were hundreds of females on the grasses and thousands of the black males flying just over them. The swarm lasted over an hour (probably prolonged because the temperature rose very slowly); even after all of the females were gone, many males were still flying up and down among the grasses.

#### FORMICA ULKEI Emery

*Formica ulkei* was more common than *F. obscuripes*. Its mounds were distributed about the George Reserve at the borders of several marshes and swamps, in much the same habitat as those at Palos Park, Illinois (Dreyer and Park, 1932). They were always near water, sometimes in open fields and sometimes at woods' edge, but never in complete shade.

Observations of flight were made for one colony in 1954 and a second colony in 1955; flight activities were checked again in 1957. The 1954 colony (field nest) was in the full sun of an open field

near the border of Fishhook Marsh. The vegetation was predominantly Canada bluegrass and trailing blackberry (*Rubus flagellaris* Willd.) with a scattering of common field plants such as bergamot (*Monarda fistulosa* L.), Indian hemp (*Apocynum cannabinum* L.), and Queen Anne's-lace (*Daucus carota* L.), and a few small black oaks (*Quercus velutina* Lam.) and choke-cherry (*Prunus virginiana* L.). The mound was the usual *ulkei* structure, a cone 12 inches high at the center and 80 inches long by 65 inches wide. It was bare on top and had a sparse growth of Canada bluegrass along its sloping sides.

The other colony (road nest), studied in 1955, was in a more shaded location. It stood at the side of a road between Fishhook Marsh and Southwest Swamp and was at the edge of one of the oak-hickory woods. Sun came from the south, across the road and the swamp beyond. The cone was a large symmetrical one, 25 inches high and 90 inches in diameter.

In 1954, flights were watched at the field nest for seven consecutive days (July 8 to 14) — probably not the entire period during which flight occurred. In 1955, four flights were studied at the road nest (June 26 to 29), and it is known that flights occurred before and after that period.

The road colony, an old one, produced a prodigious number of winged ants. The four flights were similar in pattern. Males and females came out of nest openings early in the morning, moving slowly in the cool air, among workers which paid no attention to them. At first they wandered about on the mound; then many began to go down to the ground around it and to climb grass blades and other low plants.

Soon males were thick on the mound, and dark masses of them were pouring from the lower nest exits and climbing vegetation, until they were numerous on grasses around the nest and on plants behind the nest for a distance of six feet. In the meantime, flying had begun, with ants flying first from little patches in the sun, while shaded parts were still too cold; then, as temperature rose, flight occurred from the whole area of mound and vegetation. Soon the air was full of the black males, and hundreds were taking off each minute. Most males fluttered their wings vigorously before flying. Sometimes they failed to fly, dropped, and climbed again. Some flew off into the distance at about head height, while others rose almost straight up as far as the eye could follow. Most flew east or south-east across the swamp toward the source of the greatest light, and their wings glistened in the sun as they rose. Thousands of males flew; yet there seemed to be an inexhaustible supply still coming from the nest.

Females were much less numerous and behaved quite differently. They walked down off the mound and continued walking until they were lost from sight in the vegetation. Once a male was seen mating with one on the road, but usually the females were ignored. A few climbed vegetation near the nest, fluttered their wings and then

climbed down. No females were seen to fly from this nest, but from other observations, it seems probable that they walked to shrubs or trees and climbed to considerable heights before flying.

Flights at the field nest showed a few differences. As this was a smaller colony, flights were not so heavy; still, hundreds of males were seen to fly each day. At this nest very few males flew from the mound, probably because it was in the sun and warmed quickly, but they flew from vegetation all around the mound. Since the nest was in the open, they were not so likely to fly in one direction, and on an overcast day they flew at random in all directions. During the male flights, females were seen walking down off the mound. Soon they began climbing plants a yard or two from the nest. They avoided grasses, which seemed too frail for their weight, and gathered on such plants as goldenrod, bergamot, and small cherry shrubs. They would walk back and forth on the plants, stop and flutter their wings, walk some more, flutter again, and at last fly. Their hesitance to fly and their habit of walking long distances on the ground was puzzling. Perhaps some females enter neighboring mounds without flying at all. Once one was seen being pulled toward a nest by a group of workers, but no other indication of adoption was found.

Flights ended in essentially the same manner each time. Flying would lessen, fewer winged ants would come from the mound, and many on grass blades would walk down and back into the nest. Ordinarily workers paid no attention to winged ants, but some workers would pull them toward nest entrances as flights slackened. Females usually managed to free themselves, but males were often dragged to entrances and escorted down.

Studies made in 1957 showed that the *F. ulkei* flights began soon after the first males and females emerged from the pupal stage, and continued on each suitable day until all had emerged and flown.

Records of time of day and the temperature at which flights occurred are given on Table II. It will be noted that flights took place early in the morning, the time of starting and duration being determined primarily by temperature. Generally males and females began coming from nest openings when the temperature was still in the low 50's (sometimes at gray dawn), and males would start flying at 59° or 60°F., provided the light was bright enough. Height of flight usually took place between 60° and 73°F. and length of flight varied from thirty-five minutes (cut short by darkening sky) to one hour and forty minutes. Usually ants did not fly at temperatures above 76°F., and sometimes flights stopped at temperatures well below this. Increasing cloudiness ended flights. Flights apparently were prevented by night temperatures which were too warm. On June 30 and July 1, when temperatures were 71°F. and 70°F. at 5:00 a.m., no winged ants came out at all, although flights were renewed after that when the nights were cooler.

In 1957, these two colonies and three others in the vicinity were

checked to determine the total number of flights of a colony. The first callow males and females were found inside the field nest on June 20. The first flight took place ten days later. At this time there were still many pupae and only a few winged ants in the nest. Some pupae were darkened and ready to emerge, but most were still white. This colony was in thriving condition and had eleven flights which occurred between June 30 and July 15. During that time flights were prevented on four days by rain and on one day by high wind. Activities of flights and temperatures at which flying took place did not vary from those of 1954. Both males and females were abundant. In contrast, the road nest had deteriorated. It had only four flights (July 10 to July 16), and no females were seen.

The beginning dates of flights in the five colonies observed varied by ten days. Two began flights on June 30, one on July 3, and two on July 10. Each flew on every favorable day until the supply of winged ants was exhausted. (July 5, 8, 11, 12, and 13 were the unfavorable dates). The number of flights and terminative dates also varied greatly. The field nest had eleven flights, the road nest only four. The third colony was a large vigorous one which had twelve flights (June 30 to July 16), the fourth had five flights (July 3 to July 10), and the fifth began flying on July 10 and had six flights by the 18th, when observations ceased.

#### SUMMARY

Flights of the ants *Formica ulkei* and *Formica obscuripes* were watched at the Edwin S. George Reserve, Livingston County, Michigan during the summers of 1954, 1955, and 1957. Each species had numerous, extensive flights which occurred in late June and early

TABLE II.—Flights of *Formica ulkei*

Date	Beginning	Height of flight	End
Field nest			
7-8-54	59° 7:45	72° 8:10 - 73° 8:35	76° 9:05
7-9-54		66° 7:30 - 69° 8:15	76° 8:25
7-10-54	63° 7:20	65° 7:35 - 65° 8:40	67° 8:45
7-11-54	63° 7:20	65° 7:25 - 66° 7:35	70° 7:55
7-12-54	64° 5:50	65° 6:00 - 66° 6:30	69° 6:50
7-13-54		67° 6:00 - 70° 6:20	72° 6:30
7-14-54	62° 5:20	62° 5:45 - 63° 6:00	
Road nest			
6-26-55	59° 7:15	63° 7:35 - 72° 8:30	68° 8:45
6-27-55	60° 7:25	65° 7:50 - 67° 8:25	68° 8:30
6-28-55	60° 6:25	62° 7:00 - 72° 7:40	72° 8:05
6-29-55		64° 6:10 - 65° 7:00	67° 7:15

Temperature in degrees F.; time a.m.

July. In each case beginnings of flights were determined by temperature: *F. ulkei* started to fly at 59° to 60°F. and *F. obscuripes* at 69° to 70°. Thus flights occurred very early in the morning after warm nights and later in the morning after cold ones. In both species large numbers of males flew from grasses around the nest. Females of *F. obscuripes* flew as readily as did the males, but *F. ulkei* females had a harder time getting into the air. They walked on the ground for considerable distances, avoided the frail grasses and flew from trees, shrubs and the sturdier herbs.

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## Intra-Specific Variation in the Bigmouth Shiner (*Notropis dorsalis*)<sup>1</sup>

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Meristic characters, such as the number of fin rays or scales, form an important group of taxonomic characters used to distinguish species and subspecies of fish. The variability of such characters and the factors that determine their numbers have been important fields of investigation for over 70 years. Excellent reviews of the voluminous literature pertaining to the variability of meristic characters have been presented by Hubbs (1934, 1940) and Tåning (1952). More recently Bailey and Gosline (1955) have examined the problem of variability in the number of vertebrae in the family Percidae. In general the consensus of opinion has been that the variability and variation observed have a direct environmental origin, although certain workers (Schmidt, 1918; Heuts, 1947, 1949) have presented evidence that the observed variation may well have a genetic origin. If the variation observed and reported in many species is actually due to direct environmental effects on the developing individual, quite possibly many subspecies may in reality be "ecophenotypes" and unworthy of taxonomic recognition. The above conclusion has been reached in respect to subspecies of certain minnows and darters by Bailey and Gosline (1955) and Bailey, Winn and Smith (1954).

The present problem was undertaken to determine the amount and nature of the intra-specific variation of certain meristic characters in the bigmouth shiner (*Notropis dorsalis*).

### METHODS

During the summers of 1952-1956, 1,080 specimens of the bigmouth shiner were collected and examined. The above specimens were taken by means of quarter-inch mesh seines in streams tributary to the Minnesota, St. Croix, Mississippi and Missouri rivers in Minnesota.

The characters listed below were measured in the manner outlined by Hubbs and Lagler (1949): scales in the lateral line, scales

<sup>1</sup> This research was supported in part by a grant from the Research Fund of the University of South Dakota.

above and below the lateral line, scales before the dorsal fin, scales on the caudal peduncle, rays in the dorsal, anal, pectoral and pelvic fin. Statistical analyses followed those outlined by Simpson and Roe (1939) and Snedecor (1946).

There are a number of important sources of error in any study of variation: systematic errors, sampling error or bias, sexual dimorphism, etc. To determine whether any change in counting took place while working on a sample, the averages for individual groups of 35 specimens selected at random from a sample of 212 individuals from the South Branch of the Zumbro River were compared with each other and with the average for the entire sample. The individual sample averages presented in Table I indicate that there was no significant change in the method of counting during the study of the sample. The value for scales on the caudal peduncle was low in the sixth group, but this is believed to be due to chance, as one would expect one value out of 48 to be significantly different due to chance alone. A similar comparison with subsamples of 20 individuals revealed no significant differences between the subsample averages. The above comparison gave greater confidence in the averages for small samples (20-35 individuals) than might otherwise have been warranted.

As an attempt to check on sampling bias or error, a comparison was made between the averages for two samples taken on consecutive week ends from the Zumbro River. The averages for all but one character, scales before the dorsal fin, showed close agreement. The agreement in averages indicated, although it was certainly not proof, that there was little sample bias in this instance. It could in no way be interpreted as proof of the lack of bias in other samples, but it did give greater confidence in the sampling method than would have been warranted had there been greater disagreement between the samples.

Each sample was analyzed separately. In certain cases after the statistical computations had been completed on the individual samples and no differences were found, the samples were pooled; all cases in which this was done are evident in the tables and discussion.

No evidence of sexual dimorphism was found in the bigmouth shiner in so far as the characters studied were concerned. A comparison of 81 females and 131 males in a sample from the Zumbro River (Table II) revealed no significant differences between the sexes. The above comparison was representative of similar comparisons of males and females in other samples.

#### ANNUAL VARIATION

Certain of the characters studied showed considerable annual variation. Sample averages for collections taken in the years 1952-1956 from the same station on the Credit River at Savage, Minnesota, (Table III) showed significant differences in the number of

TABLE I.—Comparison of the averages of individual samples of 35 drawn at random from a sample of 212 *Notropis dorsalis* from the South Branch of the Zumbro River, Minnesota

Group	Scales in		Scales Above		Scales Below		Caudal Peduncle Scales	Dorsal	Fin Rays in		Pelvic	Standard Length in mm
	Lateral Line	Lateral Line	Lateral Line	Lateral Line	Lateral Line	Lateral Line			Anal	Pectoral		
I	34.66 0.19 <sup>1</sup>	4.86 0.06	4.86 0.06	4.54 0.09	4.54 0.09	12.44 0.10	12.44 0.10	7.94 0.04	8.03 0.03	14.68 0.16	7.80 0.08	47.90
II	34.88	4.94	4.94	4.46	4.46	12.37	12.37	8.00	8.03	14.26	7.71	45.02
III	35.06 0.18	5.02 0.05	5.02 0.05	4.48 0.08	4.48 0.08	12.40 0.10	12.40 0.10	7.97 0.03	8.00 0.07	14.43 0.14	7.74 0.08	41.96
IV	35.31 0.23	5.09 0.07	5.09 0.07	4.46 0.08	4.46 0.08	12.37 0.11	12.37 0.11	7.97 0.03	7.97 0.03	14.12 0.14	7.91 0.05	44.72
V	35.00 0.16	4.91 0.06	4.91 0.06	4.40 0.10	4.40 0.10	12.26 0.11	12.26 0.11	7.86 0.06	7.97 0.05	14.44 0.15	7.85 0.06	46.03
VI	34.74 0.16	5.00 0.07	5.00 0.07	4.54 0.08	4.54 0.08	12.06 <sup>2</sup> 0.08	12.06 <sup>2</sup> 0.08	7.94 0.04	8.00 0.07	14.43 0.11	7.89 0.05	42.92
Total	34.94 0.08	4.97 0.03	4.97 0.03	4.49 0.04	4.49 0.04	12.30 0.04	12.30 0.04	7.95 0.02	8.00 0.02	14.47 0.06	7.82 0.03	44.76

<sup>1</sup> Represents standard error.

<sup>2</sup> Difference from average highly significant ( $p = 0.01$ ).

scales above and below the lateral line. Another group of characters, the number of rays in the dorsal, anal and pelvic fin, exhibited little annual variation and low variability.

The variation in the number of lateral line scales, pre-dorsal scales, scales on the caudal peduncle, and the number of rays in the pectoral fin was intermediate to that displayed by the previously mentioned groups of characters.

The high variability and extreme variation in the number of scales above and below the lateral line indicate that caution is necessary in their use in intra- and inter-basin comparisons. The group of characters exhibiting an intermediate level of annual variation is of greater interest, particularly the number of scales in the lateral line. In respect to the latter character there is a difference between the 1954 average and the averages for 1952 and 1955 of over 0.6 of a scale. The 1954 average does not differ from either 1953 or 1956 average and in turn the 1952, 1953, 1955 and 1956 averages do not differ significantly from one another. When all five samples are combined in an analysis of variance, the probability that the differences between the means is due to chance is less than 1 in 1000. The significance of these annual differences is difficult to ascertain since they were not correlated with any perceptible ecological changes in the five-year period. A suggestion of a cyclical phenomenon is evident in the averages, but is not warranted with so few annual samples. Differences such as those mentioned do take on some significance when intra- and inter-basin comparisons are made. Differences of this magnitude in samples from the same station taken in different years suggest that caution is necessary before statistical differences can be accepted as a criterion for defining micro-geographic races.

TABLE II.—Variation of nine meristic characters in males and females from the Zumbro River

Character	N	Males	N	Females
Scales in Lateral Line	131	34.89±0.09	81	35.02±0.15
Scales Above Lateral Line	131	4.92±0.03	81	5.00±0.04
Scales Below Lateral Line	131	4.45±0.05	81	4.57±0.06
Scales Before Dorsal Fins	131	22.02±0.19	80	22.42±0.26
Caudal Peduncle Scales	130	12.31±0.05	81	12.30±0.06
Dorsal Rays	131	7.96±0.02	81	7.92±0.03
Anal Rays	131	8.01±0.03	81	7.97±0.03
Pectoral Rays	131	14.48±0.08	80	14.45±0.08
Pelvic Rays	131	7.83±0.03	80	7.80±0.05

TABLE III.—Averages for meristic characters in *Notropis dorsalis* from the same station on the Credit River in the years 1952 to 1956

Character	1952 (25)	1953 (36)	1954 (30)	1955 (23)	1956 (34)	1952-1956
Scales in						
Lateral Line <sup>1</sup>	34.97±0.20	35.25±0.17	35.60±0.22	34.96±0.21	35.32±0.15	35.24±0.09
Scales Above						
Lateral Line	5.88±0.11	5.33±0.08	5.53±0.09	5.13±0.07	5.47±0.08	5.47±0.04
Scales Below						
Lateral Line	4.60±0.05	4.69±0.08	4.17±0.07	4.30±0.08	4.74±0.11	4.51±0.04
Caudal Peduncle						
Scales	12.41±0.10	12.39±0.11	12.73±0.19	12.91±0.20	12.85±0.15	12.64±0.07
Dorsal Fin Rays	7.96±0.04	8.09±0.04	8.00±0.00	7.96±0.04	8.00±0.00	8.01±0.02
Anal Fin Rays	7.92±0.05	8.19±0.11	8.03±0.03	8.00±0.00	8.00±0.06	8.03±0.02
Pectoral Fin Rays	13.84±0.16	13.94±0.13	14.07±0.10	13.52±0.16	13.62±0.14	13.81±0.06
Pelvic Fin Rays	7.72±0.09	7.81±0.06	7.80±0.07	7.96±0.04	7.85±0.06	7.82±0.03
Scales Before						
Dorsal Fin	22.16±0.46	23.22±0.43	22.30±0.44	19.91±0.96	22.65±0.46	22.21±0.26

<sup>1</sup> 1952±1953±1956± 1952—1956 average, 1954±1953±1956± 1952—1956 average,  
1954 average significantly different ( $p=0.04$ ) from 1952 and 1955 averages

TABLE IV.—Intra-stream variation in the number of scales in the lateral line, caudal peduncle scales and the number of rays in the pectoral fin of *Notropis dorsalis* from three tributaries of the Zumbro River

Tributary	N	Scales in Lateral Line	Caudal Peduncle Scales	Pectoral Fin Rays
North Branch	40	$35.51 \pm 0.21^1$	$12.35 \pm 0.09$	$14.45 \pm 0.15$
South Middle Branch	62	$34.53 \pm 0.18^2$	$12.37 \pm 0.07$	$14.40 \pm 0.10$
South Branch	212	$34.94 \pm 0.08$	$12.30 \pm 0.04$	$14.47 \pm 0.06$
Total		$34.94 \pm 0.07$	$12.33 \pm 0.03$	$14.45 \pm 0.05$

<sup>1</sup> Difference from both South Middle and South Branch averages highly significant.

<sup>2</sup> Significantly different from South Branch ( $p=0.04$ ).

#### INTER-STREAM VARIATION

Samples taken from three tributaries of the Zumbro River exhibited considerable variation in the number of scales in the lateral line, but little variation in the number of caudal peduncle scales and rays in the pectoral fin (Table IV). The water distances between the three stations on the tributaries were approximately as follows: North to South Branch, 80 miles; North to South Middle Branch, 60 miles; South Middle to South Branch, 20 miles. No marked ecological differences were apparent among the three tributaries that might have accounted for the differences found. Distance between stations was considered a possible factor; however, the difference between the averages for the North and South branches was less than the difference between the averages for the North and South Middle Branch samples, which were nearer one another. The sample averages for the South and South Middle branches were almost as different as between the North and South branches even though they were separated by only one-fourth the distance. It seems extremely doubtful that distance between segments of the population would in this case supply a satisfactory explanation for the differences found.

Differences within a single stream system did indicate that great caution was necessary before accepting any particular average value as that characteristic or representative for the population of an entire stream system. The fact that two sample averages from one stream system differed by almost one full scale is of some significance when intra- and inter-basin comparisons are to be made.

#### INTRA-BASIN VARIATION

When a comparison of averages for samples from the same drainage basin was made, considerable variation was found in the number of scales in the lateral line, scales on the caudal peduncle and rays in



the pectoral fin (Tables V and VI). No significant differences between sample averages were evident for the following characters: number of rays in the dorsal, anal and pelvic fins.

A particularly good example of intra-basin variation was that exhibited by the number of scales in the lateral line for samples from various tributaries of the Minnesota River (Table V). Specimens from the Redwood River had a significantly greater number of scales in the lateral line than did specimens from the Cottonwood, Little Cottonwood and Blue Earth rivers. Specimens from the Little Minnesota, Yellow Bank, Yellow Medicine, and Credit rivers also had fewer scales than the Redwood River population, but not significantly fewer, and while the former had a higher average than shiners from the Blue Earth, Cottonwood and Little Cottonwood rivers, the differences were not significant. There was no evidence of a geographic cline.

The same general pattern of variation was evident in other characters although the pattern was not the same as for the lateral line scales, and no consistent pattern was evident in the variation. The

TABLE V.—Variation in the number of scales in the lateral line, caudal peduncle scales and the number of rays in the pectoral fin of *Notropis dorsalis* from various tributaries of the Minnesota River (Streams listed in order from the headwaters to mouth.)

Stream	N	Scales in Lateral Line	Caudal Peduncle Scales	Pectoral Fin Rays
Little Minnesota	23	35.09±0.21	12.91±0.19	14.04±0.12
Yellow Bank <sup>1</sup>	39	35.10±0.15	12.70±0.12	13.65±0.08
Yellow Medicine	35	35.03±0.17	12.64±0.14	14.12±0.14
Redwood	30	35.83±0.29	13.27±0.20	14.13±0.16
Cottonwood	25	34.56±0.15	12.44±0.14	13.60±0.19
Little Cottonwood	48	34.65±0.15	12.50±0.11	14.19±0.12
Blue Earth	48	34.78±0.14	12.42±0.10	14.30±0.11
Credit River	148	35.24±0.09	12.64±0.07	13.81±0.06

<sup>1</sup> Number of specimens for caudal peduncle and pectoral fin rays counts=47 and 54 respectively.

TABLE VI.—Variation in the number of scales in the lateral line, caudal peduncle scales and the number of rays in the pectoral fin of *Notropis dorsalis* from various tributaries of the Mississippi River (Streams listed in order from Red Wing, Minnesota southward.)

Stream	N	Scales in Lateral Line	Caudal Peduncle Scales	Pectoral Fin Rays
Prairie	65	35.23±0.14	12.15±0.06	14.60±0.11
Zumbro	314	34.94±0.08	12.33±0.03	14.45±0.05
Crooked	30	35.40±0.21	12.73±0.15	14.57±0.14
Cedar	57	35.89±0.16	12.33±0.08	14.25±0.09
Des Moines	83	35.19±0.13	12.78±0.10	13.55±0.11

sample from the Redwood River had the highest average number of scales in the lateral line and scales on the caudal peduncle but was in the middle range as far as the number of rays in the pectoral fin was concerned. When a careful analysis was made, there was no evidence of a correlation between the various characters studied, although the Redwood River sample tended to have higher averages and the Blue Earth River sample lower averages. The maximum difference between samples was 1.2 scales or almost twice the annual variation found in the Credit River in a five-year period and 20 percent greater than the difference found within a single stream system.

A similar pattern of variation was discovered when averages of samples from streams tributary to the Mississippi River were compared.

To explain these differences on ecological grounds is extremely difficult. All of the streams are of approximately the same size; all flow through glacial till of the same age and the water distances between the neighboring streams are in some cases less than the distances between the North and South branches of the Zumbro River. Possibly habitat preferences tend to isolate the individual populations, for the bigmouth shiner seems to prefer small streams with shifting sand bottoms and appears to be uncommon in the large river habitat. It is quite possible that the sluggish silt-laden Minnesota River acts as a barrier to inter-stream migration and in effect isolates the individual stream populations. Starrett (1951) noted that the bigmouth shiner was subject to marked fluctuations in population size, being very common one year but scarce the following year. If such fluctuations are also characteristic of Minnesota populations, then reduced breeding numbers plus the postulated low migration rate might account for the differences exhibited in certain characters by neighboring populations. From the data in hand it seems extremely doubtful that environmental differences of sufficient magnitude exist between these streams to account for the differences found.

#### INTER-BASIN VARIATION

The same variability found within a single basin was found to exist between basins. In only a few instances did samples from a single drainage system differ significantly from all other samples. The sample from the upper Mississippi River (Table VII) had a significantly higher number of scales in the lateral line than all other samples, but as this value represented only 16 individuals no great significance could be attached to the difference found. For other samples the differences were no greater than those found between annual samples from the Credit River, and in no cases were the differences greater than those found to exist between samples from the tributaries of the Minnesota River.

Pooling of samples from the same basin did bring out differences between populations in different drainage basins (Table VII). The significance of such differences was difficult to interpret in view of the high annual and intra-basin variation that was exhibited. Theoretically, the pooling of samples would give an average value closer to the "true" mean for the population, but while this average might be of certain value, there were serious limitations to its use in this instance. It did not seem justifiable to pool samples whose means were significantly different, since these differences were taken as an indication that the samples were not drawn from a homogeneous population. Pooling would simply hide the interesting components of the variation. When basin samples were pooled, it was found that there were no marked differences in the averages for scales in the lateral line, with the exception of the upper Mississippi average previously mentioned. The sample from the St. Croix River had significantly fewer scales on the caudal peduncle than all other basin populations, which showed rather similar averages for this character. Little significance was attached to this difference, since the average for the St. Croix sample did not differ from the average for caudal peduncle scales in samples from the Zumbro River (Table IV), nor did the average differ from that of the Prairie River (Table VI). Similarly the populations from the Minnesota and lower Mississippi rivers differed significantly in the number of rays in the pectoral fin, but when the averages for the individual samples were compared (Tables V and VI) the statistical difference between the pooled samples lost its significance. The whole picture of inter-basin variation was complex and the complexity and irregularity were believed to be a reflection of the high intra-basin variation.

#### SCALES BEFORE DORSAL FIN

One character, the number of pre-dorsal scales, was given only passing mention previously but deserves further comment. The

TABLE VII.—Variation in the number of scales in the lateral line, caudal peduncle scales and the number of rays in the pectoral fin of *Notropis dorsalis* from various drainage basins in Minnesota

Basin	N	Scales in	Caudal Peduncle	Pectoral Fin
		Lateral Line	Scales	Rays
Upper Mississippi <sup>1</sup>	16	36.67±0.20	12.50±0.12	13.60±0.24
St. Croix	20	34.60±0.27	12.00±0.07	14.15±0.15
Minnesota	401	35.07±0.06	12.65±0.04	13.92±0.04
Lower Mississippi <sup>2</sup>	539	35.14±0.05	12.28±0.03	14.27±0.04
Missouri	97	35.12±0.13	12.75±0.08	13.88±0.08
Total		35.12±0.04	12.51±0.02	14.09±0.03

<sup>1</sup> Above St. Anthony Falls, Minneapolis, Minnesota.

<sup>2</sup> Below St. Anthony Falls, Minneapolis, Minnesota.

extreme range of this character was from 8 to 28 scales, the range in sample means was from  $18.61 \pm 1.05$  to  $24.31 \pm 0.42$ , and the coefficient of variation ranged from 7.0 to 13.3. The variability of this character, while of some interest, is not as important as the extreme individuals which phenotypically resembled the scaleless western form, *piptolepis*. In certain samples individuals with an apparently scaleless or partially scaled nape were found; this was particularly true of samples from the tributaries of the Minnesota and Missouri rivers. A number of individuals were at first noted as having a scaleless nape, but on closer examination a few imbedded scales were discovered. The highest percentage of individuals exhibiting this partially scaled condition in any one sample was 10 percent. While this study has been rather limited in its scope, the presence of individuals closely resembling the western form far outside its known range makes the usefulness of this character in subspecific discrimination uncertain.

#### DISCUSSION

If, during the present study, single samples had been drawn from each of the drainage basins, significant differences would have been found between the various populations. Since certain of these populations are geographically isolated from one another, this finding might have indicated a subspecific name for each of the basin populations. Such recognition would certainly have been unwarranted because when a number of samples were drawn from each of the drainage basins, it became apparent that not only were there significant differences between samples drawn from different drainage basins, but that there were also differences between populations existing within the same basin. Failure to sample adequately would have given a false impression of the nature of the inter-basin variation and no knowledge of the tremendous intra-basin variation. The findings presented indicate caution in the use of only a few samples from various drainage basins for taxonomic revisionary work and particularly in the use of only a single sample. Various rules, i.e., 75 percent rule, 90 percent rule, etc., have been proposed as criteria for defining subspecies. These rules are useful to the extent that they tend to prevent unlimited naming of segments of a variable species and in effect make the subspecies a more conservative category. The rules are however empirical, and hence do little to answer the criticism directed toward the usefulness of the trinomial. In many cases the rules are applied in an attempt to give the subspecies the objectiveness of the species, yet the rules are subjective as is the subspecies. It may be that the labor required for the analysis reported above is not commensurate with the results obtained, but it is believed that a more detailed knowledge of the amount and nature of annual, intra-stream, intra-basin, and inter-basin variation of the populations comprising

a species would go far toward giving the subspecies a better biological basis.

Many of the populations of the bigmouth shiner might be viewed as micro-geographic races, but the differences are far below the level where nomenclatural recognition is warranted. Mayr (1941) and others have already pointed out that no two populations have been found to be identical in all respects. Dice (1940) stated that "in *Peromyscus* each more or less isolated population constitutes a local race," since no two populations were ever found to be identical. The same situation seems to exist in *Notropis dorsalis*, for while all populations did not differ significantly from one another, many did. A fundamental problem is whether these differences are due to direct environmental influences on the developing embryos or whether they are due to genetic differences between the populations. Differences in the genetic composition of the populations may also reflect the effects of the environment, but in this case, the environmental influence is indirect, being due to the operation of different environmental selection pressures on the genetic variability in the populations. Hence, it is essential to know whether the populations are merely different "ecophenotypes" or whether they actually differ in their genetic composition. Where fish populations are apparently isolated from each other, as for example the populations within the Minnesota River basin, marked differences exist between the stream populations. These differences are as great as or greater than those found between populations from different drainage basins. Differences of this magnitude seem to be more easily explained on a genetic basis than by postulating environmental differences between various streams which appear to be similar, although in all probability not identical.

Temperature appears to be one of the more important factors in the environmental complex determining the number of scales in a body region or the number of rays in a fin, particularly the temperature during the "phenocritical period" of Tåning (1952). If temperature is the controlling factor, one might expect that a group of characters in the same population would tend to vary in the same direction, but experimental evidence indicates that this is not the case. Tåning has pointed out that in *Salmo trutta* the various characters are determined at different stages during embryonic development and further that there is not a simple linear relationship between the developmental temperature and the number of parts. Therefore, it is hazardous to make comparisons between different characters, but it is justifiable to compare the same characters in different populations or in the same population in different years. When such comparisons are made between populations in the Minnesota and Mississippi rivers existing under nearly identical conditions of temperature (within 70-72° isotherms), there is little correlation between populations. While genetic control over the characters is not proved by this lack

of correlation, it seems to be a reasonable alternative and is certainly consistent with certain experimental work (Schmidt, 1918; Heuts, 1947, 1949).

Bailey and Gosline (1955) have pointed out that in small streams essentially isothermal conditions prevail at any given time; hence the temperature preceding spawning differs during the phenocritical period only to the extent that it is modified by atmospheric factors. That the bigmouth shiner is restricted to small and moderate sized streams is borne out by the collecting records of the past five years and the findings of Greene (1935), Forbes and Richardson (1920) and many others. Marked shifts in temperature do occur in the small stream habitat during the spring months (May and early June) in Minnesota; therefore spring spawners might well be exposed to fluctuating temperature during their embryonic development. The bigmouth shiner is, however, a late summer spawner, spawning in July and August (Starrett, 1951). During this period of the year there are no marked atmospheric shifts, the temperature averages being similar from year to year. It would therefore seem reasonable to assume that temperature shifts would be minimal during the embryonic development of the bigmouth shiner. Intra-basin temperature differences or shifts of the magnitude used in various experimental studies ( $5^{\circ}\text{C}.$ ) are very unlikely; differences of a lesser magnitude ( $1\text{--}3^{\circ}\text{F}.$ ) probably occur. What effect such small changes or differences might have is difficult to assess, but they would not seem to account for the marked annual and intra-basin variation reported here.

If one postulates environmental control for one group of characters, scales in the lateral line, pectoral fin rays, etc., which show a high variability, then one might well expect high variability in similar characters, dorsal fin rays, anal fin rays, caudal peduncle scales, etc. This is not the case. The number of pelvic, dorsal, and anal fin rays are nearly identical from year to year in samples from the same station and in populations from different basins. It would seem reasonable to assume that the latter group of characters is only slightly affected by the existing environmental influences. If this assumption is correct, is the variation in other similar characters determined primarily by the environment or is it due to a greater degree of genetic variability in the species for these traits? It is certainly conceivable that minor differences in the micro-environments might select out slightly different gene combinations and hence that the genetic composition of such populations will become slightly different. Furthermore, the variability built up by mutation in the various populations will undoubtedly differ, and the possibility of the chance fixation or loss of genes in small breeding populations cannot be ignored. If these traits are controlled by multiple factors comparable to those studied in other species, it is not too difficult to explain the variability exhibited by certain meristic characters. However, at present it is impossible to decide from the available evidence whether meristic characters in



fishes are primarily determined by the genotype or by the direct influence of the environmental complex. The critical experiment in many cases has yet to be done; i.e., the rearing of progeny of the various variants in a common environment to see whether the differences present in natural populations are retained when exposed to similar environments.

Tåning (1952) produced "phenocopies" of the northern and southern forms of the sea trout by heat and cold shock treatment applied to the Danish sea trout. Svardson (1952) has shown that the number of scales in the lateral line can be modified by almost 11 scales when populations are transplanted to a different environment, indicating that the scale number can be modified. However, this rather wide change in scale number does not prove that scale number is not under the control of the genotype. The phenocopies of Tåning and the variation reported by Svardson could also be interpreted as an indication of the plasticity of scale number, i.e., the genotype simply determines the upper and lower limits in the number of scales. Moreover, Svardson implies that if members of sympatric populations were transplanted to different environments, they would retain the differences that existed in the original environment. Sumner (1932) found that rearing *Peromyscus* in a constant environment modified the phenotype but that the differences between subspecies were retained in the constant environment. Heuts (1949) found that progeny of given populations of the stickleback, raised under identical conditions from the egg to adult stage, retained the characteristic differences found in the populations in nature, indicating genetic control, not on the number of parts, but on the limits of variation. The conclusion that the variation exhibited is primarily genetic is not to be interpreted as ruling out the importance of the environment, but rather that it operates on the existing genotypes, modifying their expression within their reaction ranges and also selecting the better adapted genotypes. As Clausen (1951) has ably illustrated, it is not one genotype, but rather a large number of genotypes which enable the population to survive and give it the necessary adaptability to survive through periods when environmental shifts occur.

On the assumption that certain meristic characters are controlled by multiple genes, it is not surprising to find considerable intra- and inter-basin variation. Experimental support for this assumption is contained in the report of Lagler and Bailey (1947). They ascertained that the differences between two subspecies of the Johnny darter (*Etheostoma nigrum*) were genetically fixed. *Etheostoma nigrum nigrum* and *E. n. eulepis* raised under identical conditions retained characteristics used in their identification.  $F_1$  hybrids showed a phenotypic intermediacy and the authors concluded that the differences between the two subspecies could not be explained on the basis of simple dominance.

If the annual, intra- and inter-basin variation reported here for the bigmouth shiner is also characteristic of other cyprinids, it may be necessary to make more detailed studies before subspecies can be adequately delimited. The necessity for such detailed studies has been ably discussed by Bailey and Gosline (1955) and Bailey, Winn and Smith (1954). Before any final conclusion can be reached about the importance of annual variation, it is felt that annual collecting over a longer period of time may be required. If annual differences as great as those reported for the bigmouth shiner are also characteristic of other species, it would indicate that this factor must be considered before geographic races can be defined. A study currently being carried out on variation in the common shiner (*Notropis cornutus*) and the sand shiner (*N. deliciosus*) indicates that the level of annual and inter-population variability in these two species is considerably below that reported for the bigmouth shiner.

#### SUMMARY

The annual, inter-stream, intra-basin and inter-basin variation of nine meristic characters in the bigmouth shiner from the Minnesota, Mississippi, St. Croix and Missouri rivers in Minnesota was studied. The high level of inter-basin variation found is considered to be a reflection of the complex intra-basin variation and high annual variation. The characters studied fell into three categories, one showing little or no annual variation and inter-basin variation, a second group exhibited a high level of variation and the third an intermediate level of variation. The differences between sample averages could not be correlated with any marked atmospheric changes or ecological differences between the various streams from which the samples were drawn.

The central problem is to determine whether the various populations are "ecophenotypes" or micro-geographic races. The two alternatives are discussed in light of the present study and previous studies on fishes and other groups of organisms. The various populations of the bigmouth shiner studied are interpreted as micro-geographic races though at present it is impossible to decide from the available evidence whether meristic characters in fishes are primarily determined by the environmental complex or by the genotype.

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## Some Stoneflies from Santa Catarina, Brazil (Plecoptera)

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The specimens upon which this paper is based were acquired primarily by purchase from Mr. Fritz Plaumann of Nova Teutonia, Santa Catarina, Brazil, who carefully preserved material, much of it in alcohol, so that the colors are well retained. A few specimens from the American Museum of Natural History taken by another commercial collector, Mr. A. Maller, at Corupa (Hansa Humbolt) add several records. I am indebted to Dr. Mont A. Cazier for the loan of these specimens.

The bulk of the material studied belongs to the genus *Anacroneuria*, a group of interest because there is such a large number of species throughout Central and South America, each region having its quota of species. Various early authors, including Enderlein (1909), Klápálek (1921, 1922, 1923), Navás (1916, 1932a, 1932b), and Pictet (1839) described numerous species of *Anacroneuria* from Santa Catarina and nearby states, but the descriptions are largely unaccompanied by drawings. Descriptions are inadequate to place most of their species, and the shape of the female subgenital plate is rarely described. Despite these deficiencies it seems likely that most of the names represent distinct species. However, unless the type material can be found, and the color patterns are still discernible, it will be most difficult to associate material with the names. This may be possible in many instances only after a quantity of new material is taken from each type locality where definitely known.

Most species of *Anacroneuria* are difficult to identify. Reliance must be placed largely on color patterns and on the shape of the female subgenital plate. The shape of the pronotum and venation seldom offer specific characters. The male genitalia apparently have no specific characteristics. In the present material there is considerable variation in the color patterns, but the figures of head and pronotum are presented to show the general type of color pattern of the species illustrated. The key has been devised to accommodate specimens with differences in the color of the median pronotal stripe. An outstanding characteristic of the present collection is that size is relatively constant in the female specimens of each species.

The shape of the female subgenital plate is usually distorted in dried specimens. For proper study this structure must be softened and cleared in potassium hydroxide. All genitalia figured in this paper were treated with KOH.

Abbreviations used for location of specimens are the following:

AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); CAS, California Academy of Sciences; INHS, Illinois Natural History Survey; MN, Museum Nacional, Brazil; USNM, United States National Museum; SGJ, JR., Jewett Collection; WER, Wm. E. Ricker Collection.

#### FAMILY GRIPOPTERYGIDAE

##### GENUS GRIPOPTERYX PICTET

1841. *Gripopteryx* Pictet, Hist. Nat. Ins. Neurop., Perlides, p. 319.

1921. *Gripoptera* Samal, Soc. Ent. de Belg. Ann. 61:110. New synonymy.

Since there are no apparent generic characters separating *Gripoptera* Samal (1921) from *Gripopteryx* Pictet (1841), I am placing it in synonymy with the latter.

##### *Gripopteryx brasiliensis* (Samal) n. comb.

Figs. 1, 1A, 1B

1921. *Gripoptera brasiliensis* Samal, Soc. Ent. de Belg. Ann. 61:110-112, figures of head, pronotum, dorsal and ventral views of terminalia of type.

Material of this species was readily identified from Samal's excellent description and figures of the female type. The male may be described as follows.

*Male*.—Length to wing tips, 18 mm. Length of body, 15 mm. Similar in general features to female but somewhat smaller. Ninth and tenth segments rather heavily sclerotized, other abdominal segments largely membranous except at anterior borders of tergites. Tenth tergite with median heavily-sclerotized dorsal appendage, its tip forming upturned hook, barely extending beyond posterior margin of tenth tergite in normal position, but extending well to rearward when terminalia cleared. Subanal lobes heavily sclerotized, drawn out to form long, laterally-compressed appendages that turn slightly upward and are about equal in length to ninth tergite. Eighth sternite with median plate that extends over basal half of ninth sternite in cleared terminalia and in width is about third of total width of sternite. Antennae long, composed of about 13 segments. Cerci with about 28 segments. Color of body very dark brown, lighter areas on head and at bases of femora. Antennae and tarsi very dark brown.

*Collection data*.—Male allotype, Nova Teutonia, Santa Catarina, Brazil, I-56, Fritz Plaumann (CAS). Additional material taken by Mr. Plaumann at Nova Teutonia includes the following: XI-56, ♀ (CAS); XI-57, ♂, ♀ (SGJ, JR); 21-XII-48, ♀ (SGJ, JR).

##### *Gripopteryx neofriburgensis* Navás

Fig. 2

1916. *Gripopteryx neofriburgensis* Navás, Brotéria: Série Zoológica 14:27-28, figures of the wings and terminalia of the male type.

*Male*.—Apparently the type of this species is not available for study, as Aubert (1956:438) was unable to locate it. However, the male specimens listed below agree, essentially, with Navás's figures. The basal area between the arms of the dorsal terminal process varies in width, but one specimen matches Navás's figure very closely. The tips of the two arms of this process turn downward more abruptly, however, than he illustrates.

*Female*.—Length to wing tips, 11.5-13 mm. Length of body 10-11.5 mm. Similar in general features to male with heavy pigmentation along wing veins, particularly along nearly transparent cross veins in forewings, cells with clear central areas. Length of dark brown antennae about equal to length of body without head. Dark brown cerci with 12-14 segments, nearly as long as segments 8 to 11.

Eighth sternite modified to form heavily sclerotized and pigmented sub-genital plate which extends over basal part of ninth sternite. Seventh sternite with pair of widely spaced, large swellings or knobs near outer distal margin. Ninth sternite largely membranous as are other sternites but with marginal pigmented areas along both sides.

*Collection Data*.—Female *allotype*, 4 males, 5 females, Nova Teutonia, Santa Catarina, Brazil, XI-57, Fritz Plaumann (*allotype* female, 2 males, female, CAS, 2 males, 3 females, SGJ, JR). Additional material taken by Mr. Plaumann at Nova Teutonia includes the following: X-55, ♀ (SGJ, JR), X-13-48, ♂ (SGJ, JR), XI-4-55, ♀ (SGJ, JR).

#### *Griopteryx* sp.

A second species of this genus of about the same size as *G. neofriburgensis* is represented by a single male and a single female from Nova Teutonia. These are in the writer's collection. Both are somewhat teneral and have lightly fumose wings without any spotting. The female does not appear to have a distinctive subgenital plate. The male has a very short dorsal terminal process with small, sharply-pointed arms of the furcate tip pointing abruptly downward. There is a small median, sclerotized process, hook-shaped, the tip upturned.

Until types of described species of Brazilian *Griopteryx* can be critically studied, it seems inadvisable to propose new specific names in this genus.

#### FAMILY PERLIDAE

##### SUBFAMILY ACRONEURINAE

#### *Kempnyia fusca* (Navás) New Comb.

Figs. 3, 3A, 3B

1932. *Nedanta fusca* Navás, Rev. Chil. de Hist. Nat. 36:86-88, figures of male and female terminalia of types.

1932. *Nedanta fulvata* Navás, *ibid.*, 36:88. New synonymy.

Aubert (1956:437) has reported that the types of Navás's three species of *Nedanta* were lost at the Hamburg Museum during the



second World War. Navás's figures and descriptions indicate that his species belong to the genus *Kempnyia* Klapálek (1916). His species *fulvata* was distinguished by minor color and venational characters that readily fall within expected normal range of variation in species of this genus. I am therefore treating that name as a synonym. His third species, *Nedanta isosceles*, may represent a distinct species since its ocelli are said to be arranged in an isosceles instead of an equilateral triangle.

Following is a description of this species based on material listed below.

Length to wing tips, 16.5-19.5 mm in male, 23-24 mm in female. Length of forewing, 14.5-16 mm in male, 18.5-20 mm in female.

Head mostly brown, usually with well-formed yellow M-line and bright yellow area between and behind rear ocelli, sometimes head entirely dark brown; darkest brown in interocellar area; clypeus light; appendages and rear of head brown. Pronotum brown, usually with irregular, median yellow stripe that occupies seventh to sixth of width of pronotum, sometimes pronotum entirely dark brown. Legs usually sharply bicolored with basal half of femur yellow, occasionally legs entirely brown (females). Tails brown. Wings fumose brown.

*Female*.—Subgenital plate broadly rounded and extending to half length of eighth sternite, with shallow median notch.

*Male*.—With typical modified ninth sternite bearing median, elongated keel distally. Aedeagus with heavily sclerotized structure.

*Collection Data*.—Following collected by Mr. Fritz Plaumann at Nova Teutonia, Santa Catarina, Brazil: 26-X-55, ♀ (SGJ, JR), 5-XI-55, ♂ (CAS), XI-56, ♂ (SGJ, JR), I-56, ♂, ♀ (BMNH). Following collected by A. Maller at Corupa (Hansa Humbolt), Santa Catarina, Brazil: IX-45, ♂ (AMNH), X-46, ♂, ♀ (SGJ, JR), XII-44, ♀ (AMNH).

The material from Corupa is very dark on head and pronotum, but the legs are strongly bicolored. The aedeagus of the male is identical in the two lots.

A careful study of all of the existing type material of Brazilian *Kempnyia* is needed to determine the number of described forms. The aedeagus is suggested for special consideration as this organ has sclerotized areas and structures that are very specific.

#### *Laeissa colossica* Navás

##### Fig. 4

1934. *Laeissa colossica* Navás, Acad. de Cien. Midrid, Rev. 31:22-23, figures of head and male terminal segment.

This species is represented by two female specimens from Corupa (Hansa Humbolt), Santa Catarina, Brazil, collected by A. Maller, II-46 (AMNH, SGJ, JR). The female possesses a huge, unnotched, vault-like subgenital plate that encloses the terminal segments.

Aubert (1956:439) reports that the type of this species has been lost. Until a male is available for studying the genitalia, particularly

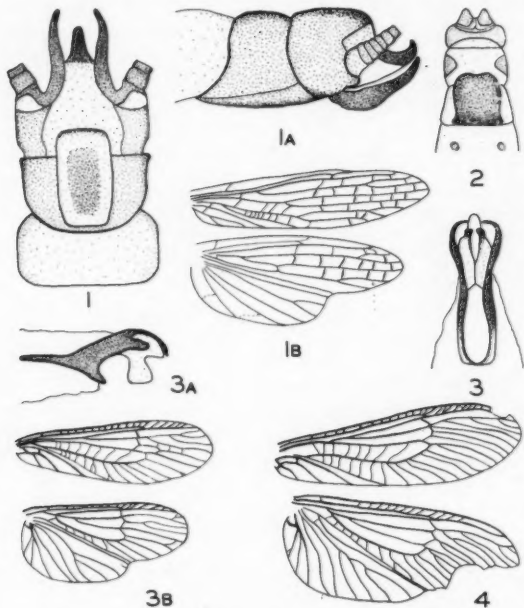
the aedeagus, it will not be possible to compare *Laeissa* with *Kempnyia* and related genera.

*Anacroneuria oculatila* n. sp.

Figs. 5, 5A

Length of forewing, 10 mm in male, 12-14 mm in female.

Head mostly brown with irregular, yellow-orange central area, clypeus and anterior part of frons somewhat lighter, markedly so in male. Pronotum brown with rather narrow central yellow (as in holotype and allotype) or light brown stripe that occupies one-seventh to about one-sixth of pronotal width. Legs brown and yellow; tibiae brown; fore femur brown with some yellow near base in female, males with basal one-fourth mostly yellow; middle femur third (female) to almost half (male) light yellow basally; hind femur at least half (female) to three-fifths (male) light yellow basally; dorsally some brown at base of femora; colored areas on middle and hind femora sharply



Figs. 1-4.—1. *Gripteryx brasiliensis*, male terminalia, ventral view; 1A, lateral view; 1B, wings of female. 2. *Gripteryx neofriburgensis*, female terminalia, ventral view. 3. *Kempnyia fusca*, male aedeagal structure, dorsal view; 3A, lateral view; 3B, wings of female. 4. *Laeissa colossica*, wings of female.

delimited. Tails dark brown except for yellow basal segment (holotype and allotype); in light specimens segments 1 to about 10 dark, succeeding ones bicolored to near tip where last few are brown. Wings fumose with brown veins except for hyaline spot in middle of wing near tip in both wings, in size spot from slightly less than area of head to about one and one-half times as large; costal vein lighter than other veins.

*Female*.—Subgenital plate four-lobed, lateral notches about as deep as median notch. Sclerotized area of ninth sternite T-shaped, long hairs on either arm of T.

*Male*.—With typical small nail on ninth sternite; wings darker than in female; smaller in size than female; markings on head more sharply defined than in female.

The color pattern of the head, especially the well-defined yellow-orange area, together with the bicolored middle and hind femora and the clear spots in the wings distinguishes this species.

*Collection Data*.—Female *holotype*, male *allotype* and 3 female *paratypes*, Nova Teutonia, Santa Catarina, Brazil, XI-56, Fritz Plaumann (CAS). Additional *paratypes* with same data as holotype except for dates are as follows: X-56, 3 ♀ (SGJ, JR); 13-X-48, ♀ (SGJ, JR); 23-X-55, 2 ♂ ♀ (SGJ, JR); 24-X-48, ♂ ♀ (MN); 24-X-55, 2 ♂ ♀ (BMNH); I-56, 5 ♀ (CAS, INHS, USNM).

*Anacroneuria aurata* n. sp.

Fig. 9

Length of forewing, 15 mm in female holotype.

Head orange-yellow, darkest between and anterior to ocelli, tubercles lateral and anterior to ocelli lighter and forming isosceles triangle; M-line almost indistinguishable. Antennae and palpi brown, contrasting strikingly with yellow color of head. Ocelli black. Pronotum dark orange-yellow with suggestion of light brown pigment over-all; no well-defined median stripe. Legs brown, contrasting sharply with orange-yellow to yellow of body and wings. Tails broken in holotype, but colored brown of same intensity as that of legs and antennae. Wings hyaline, strongly tinted with orange-yellow.

*Female*.—Subgenital plate four-lobed, lateral notches very shallow, more pigmented than sternites 1 to 7. Sclerotized area of ninth sternite with strongly pigmented T, the arms of which bear stout, dark, modified hairs.

*Male*.—Unknown.

The strongly contrasting dark color of the appendages against the orange-yellow body color, together with the female genitalia, readily separates this species.

*Collection Data*.—Female *holotype*, Nova Teutonia, Santa Catarina, Brazil, I-56, Fritz Plaumann (CAS).

*Anacroneuria tinctilamella* n. sp.

Figs. 7, 7A

Length of forewing, 11 mm in male, 11-12 mm in female.

Head yellow with distinctive pattern; clypeus bordered basally with dark brown. Pronotum brown, usually with narrow, median, yellow stripe at most sixth of pronotal width, that may, however, be obliterated with brown pigment (but not in holotype). Legs brown throughout. Tails brown. Wings lightly fumose brown in both sexes, costal vein almost colorless from its base to junction with subcosta.

*Female*.—Subgenital plate four-lobed, median notch only slightly larger than lateral notches; brown colored in strong contrast to light yellow tenth sternite. Ninth sternite with strongly pigmented T that is without modified hairs; dark distal border contracts strongly with light colored tenth sternite.

*Male*.—Not definitely known.

The brown legs, pigmentation of the female genitalia, and head color pattern readily separate this species.

A male specimen, provisionally placed with this species, has nearly concolorous legs, but the head pattern approaches that of *A. fuscicosta*.

*Collection Data*.—Female *holotype* and 27 female *paratypes*, Nova Teutonia, Santa Catarina, Brazil, XI-55, Fritz Plaumann (holotype and 10 paratypes CAS, other paratypes MN, AMNH, BMNH, INHS, USNM). Additional *paratypes* with same data as holotype except for dates are as follows: X-56, 2 ♀ (SGJ, JR); XI-56, ♀ (SGJ, JR); 5-XI-55, 10 ♀ (SGJ, JR); 6-XI-55, 8 ♀ (CAS); 7-XI-55, 14 ♀ (SGJ, JR); 8-XI-55, 14 ♀ (USNM); 9-XI-55, 14 ♀ (BMNH, INHS); 1-56, 7 ♀ (SGJ, JR).

*Anacroneuria plaumanni* n. sp.

Fig. 13

Length of forewing, 13.5 mm in male allotype, 18 mm in female.

Head mostly dark but with well-defined, large M-line; light tubercles lateral and anterior to ocelli; and light areas between and laterally rearward of the ocelli. Pronotum with bright yellow median stripe that occupies nearly one-fifth of total width. Female pronotum with angulation on sides about third of way posteriorly (due to normal hardening of the prothorax), absent in male allotype. Legs mostly brown; basally some yellow on femora, colors blending gradually. Tails with first few basal segments yellow brown, others bicolored. Wings hyaline, tinted with brown, veins evenly pigmented.

*Female*.—Subgenital plate four-lobed, lateral notches shallower than median notch, very similar to that of *A. fuscicosta*. Sclerotized area of ninth sternite with well-marked T bearing long, modified hairs on either arm, as in *A. fuscicosta*.

*Male*.—Normal with small conical nail on ninth sternite; tails and legs darker brown than those of female.

Size, the clear yellow pronotal stripe, and the brown legs distinguish this species.

*Collection Data.*—Female *holotype* and 1 female *paratype*, Nova Teutonia, Santa Catarina, Brazil, XI-55, Fritz Plaumann (CAS). Male *allotype*, same data as *holotype* except X-56 (CAS). A female *paratype* with same data as *holotype* except 24-X-55 (SGJ, JR).

*Anacroneuria trimacula* n. sp.

Fig. 11

Length of forewing, 16-17 mm in female.

Head with striking color pattern, principle feature of which is three well-defined light areas, two at either outer border of ocelli and one anterior to them. Pronotum with bright yellow median stripe not sharply delimited but occupying as much as fifth of pronotal width. Legs brown and yellow; tibiae brown; anterior femur brown except for basal, irregular yellow area that may occupy quarter of length; middle femur third to half yellow basally; hind femur with about basal three-fifths yellow; colored areas not sharply delimited. Tails with basal 12 to 13 segments brown, remaining ones bicolored except for distal few which are brown. Wings hyaline, stained with brown, costal vein somewhat lighter than other veins.

*Female.*—Subgenital plate four-lobed, lobes on same plane, notches approximately same size, but median notch slightly deeper in some specimens (but not in *holotype*). Ninth sternite with well sclerotized "T" and long, coarse hairs on each arm of it.

*Male.*—Unknown.

Size, the striking head pattern, and yellow pronotal stripe separate this species.

*Collection Data.*—Female *holotype* and 3 female *paratypes*, Nova Teutonia, Santa Catarina, Brazil, X-56, Fritz Plaumann (*holotype* CAS, other *paratypes* to INHS, USNM, SGJ, JR). Additional *paratypes* with same data as *holotype* except for dates are as follows: 7-X-55, 3 ♀ (BMNH); 11-X-55, 5 ♀ (USNM, SGJ, JR); 23-X-55, ♀ (SGJ, JR); XI-55, ♀ (SGJ, JR); 7-XI-55, 3 ♀ (INHS); 1-56, ♀ (MN).

*Anacroneuria fuscicosta* (Enderlein)

Figs. 8, 8A

1909. *Neoperla costalis* var. *fuscicosta* Enderlein, Ges. f. Naturf. Freunde Sitzber. 3:178.

Length of forewing, 10-11.5 mm in male, 12-16 mm in female. Head with irregular dark area on yellow ground color; front of frons and clypeus lightest; M-line usually interrupted to form three bright yellow spots, but may be entirely yellow. Pronotum with narrow, yellow, or brownish-yellow, median stripe that occupies as much as sixth of pronotal width. Tails brown throughout or with bicolored segments toward tips. Legs brown and yellow; tibiae brown; anterior femur largely brown, light on basal fifth in some specimens; middle femur about half yellow basally on side, less dorsally; hind femur half to two-thirds yellow basally; colors most sharply delimited on hind femur. Wings hyaline, tinged with brown, lightly fumose in males and occa-

sionally in females; subcosta and radius thicker and darker in color than other veins.

*Female*.—Subgenital plate of female four-lobed, median notch somewhat deeper than lateral notches. Sclerotized area of ninth sternite with conspicuous "T," arms of which bear stout, modified hairs.

*Male*.—Normal, with small conical nail on ninth sternite; smaller in size than female.

The above description applies to the material listed below which may be distinguished by the combination of the head color pattern, leg coloration, pronotal stripe, and shape of female subgenital plate.

This material is associated with Enderlein's species on the basis of the dark subcostal and radial veins, the dark pattern associated with *A. costalis* to which Enderlein believed it to be related, and on size. (It is highly improbable that *A. costalis* (Pictet) occurs in Brazil, as the type is from Vera Cruz, presumably the Mexican State.)

*Collection Data*.—The following material was taken at Nova Teutonia, Santa Catarina, Brazil, by Fritz Plaumann: X-56, ♀ (SGJ, JR); 7-X-55, ♂ (USNM); 23-X-55, 2♂ (SGJ, JR); 24-X-48, 2♂, 2♀ (CAS); XI-55, 2♀ (MN); XI-56, 2♂ (MN); 12-XI-55, ♀ (INHS); I-56, ♂, 11♀ (SGJ, JR, INHS, WER).

Additional material provisionally identified as this species, differs in several respects. Two female specimens have large clear spots in the wings like *A. oculatula*, and the median pronotal stripe is light brown with the median groove finely bordered by dark brown pigment. Three rather small female specimens have sharply delimited, bright yellow median pronotal stripes, and the dark area on the head is quite diffused. Several other specimens of both sexes have the median pronotal stripe brown, several with the median groove bordered by dark brown pigment of variable width. The head pattern on these latter specimens is fairly typical. Several have faint suggestions of clear areas in the wings. If this series is correctly identified as one species, it is quite possible that several existing names applied to specimens of *Anacroneuria* from southeastern Brazil should be associated with them. Additional long series from restricted areas in the region might solve this problem.

#### *Anacroneuria ampla* n. sp.

Fig. 10

Length of forewing, 19-20 mm in female.

Head strikingly patterned in yellow and brown, pattern somewhat variable but with broken M-line; yellow areas lateral to ocelli and one anterior, three forming isosceles triangle; clypeus with gray area medially. Pronotum predominantly brown, darkest along margins of sides and with rather narrow, yellow, median stripe that occupies less than fifth of pronotal width. Legs brown, lightest on underside of femora. Tails brown throughout, except in lightest specimens which have segments of distal half bicolored (but not in holotype). Wings hyaline, stained with brown to fumose brown.



*Female*.—Subgenital plate with small median notch and only suggestion of lateral notches in most specimens, similar to that of *A. aurata*. Sclerotized area of ninth sternite with well marked T and coarse hairs on either arm of it.

*Male*.—Unknown.

The color pattern of the head together with the shape of the female subgenital plate and size separates this species.

*Collection Data*.—Female *holotype* and one female *paratype*, Nova Teutonia, Santa Catarina, Brazil, XI-55, Fritz Plaumann (CAS). Additional *paratypes* with same data as *holotype* except for dates are as follows: 7-X-55, ♀ (MN); 6-XI-55, ♀ (INHS); 8-XI-55, 3♀ (SGJ, JR); 9-XI-55, 2♀ (BMNH); 1-56, ♀ (CAS); X-56, 6♀ (USNM, SGJ, JR).

*Anacroneuria impensa* n. sp.

Fig. 12

Length of forewing, 23-24 mm in female.

Head with rather indistinct markings and considerable light area as follows: posterior to ocelli except that rear corners are darkly pigmented; most of M-line; anterior part of frons and clypeus. Pronotum with broad, rather poorly defined, yellow median stripe that occupies nearly quarter of width of pronotum. Legs yellow and brown, colors blending; tibiae brownish; basal part of fore femur, about basal half of middle femur, and about two-thirds of rear femur yellowish. Tails with basal segments yellow brown, gradually becoming bicolored distally. Wings hyaline, lightly tinted with brown; costal vein little, if any, lighter than other veins.

*Female*.—Subgenital plate four-lobed, lateral notches shallower than median notch, similar to that of *A. trimacula*. Sclerotized area of ninth sternite with well pigmented T with long, modified hairs on either arm of T, as with *A. trimacula*.

*Male*.—Unknown.

Size is the principal feature distinguishing this species from *A. trimacula*, but the head markings are also much less definitive.

*Collection Data*.—Female *holotype*, Nova Teutonia, Santa Catarina, Brazil, 9-XI-55, Fritz Plaumann (CAS). A female *paratype* with same data as the *holotype* except that it was taken 6-X-55 (SGJ, JR).

*Anacroneuria badilinea* n. sp.

Fig. 14

Length of forewing, 18-20 mm in female.

Head with conspicuous dark mark originating at dark ocellar area and extending forward and laterally; yellow M-mark behind darkish anterior area; edge of frons light. Pronotum yellow and brown with irregular, mostly narrow, median brown stripe which may be finely bordered with yellow; discs mostly yellowish with blotches of brown pigment; rugosities yellowish. Legs brown and yellow; tibiae brownish-yellow; fore femur at most third yellowish basally; middle femur

less than half yellowish basally; hind femur about three-fifths yellow basally; colored areas blending. Tails with basal 12 to 14 segments yellow-brown, remaining ones bicolored except distal two or three which are dark brown. Wings hyaline, tinged strongly with brown, veins brown, those of costal area lightest.

*Female*.—Subgenital plate four-lobed, very similar to that of *A. fuscicosta* in shape, lightly pigmented. Sclerotized area of ninth sternite lightly pigmented, with coarse hairs on arms of T.

*Male*.—Unknown.

Size and the color pattern of the head and pronotum distinguish this species.

*Collection Data*.—Female *holotype* and 2 female *paratypes*, Nova Teutonia, Santa Catarina, Brazil, X-56, Fritz Plaumann (CAS). Additional *paratypes* with same data as holotype except for dates are as follows: 7-X-55, 2 ♀ (INHS); 11-X-55, 6 ♀ (SGJ, JR); XI-55, 2 ♀ (USNM); 7-XI-55, ♀ (MN); I-56, 2 ♀ (AMNH).

*Anacroneuria novateutonia* n. sp.

Figs. 6, 6A

Length of forewing, 9.5-11 mm in male, 13.5 mm in female.

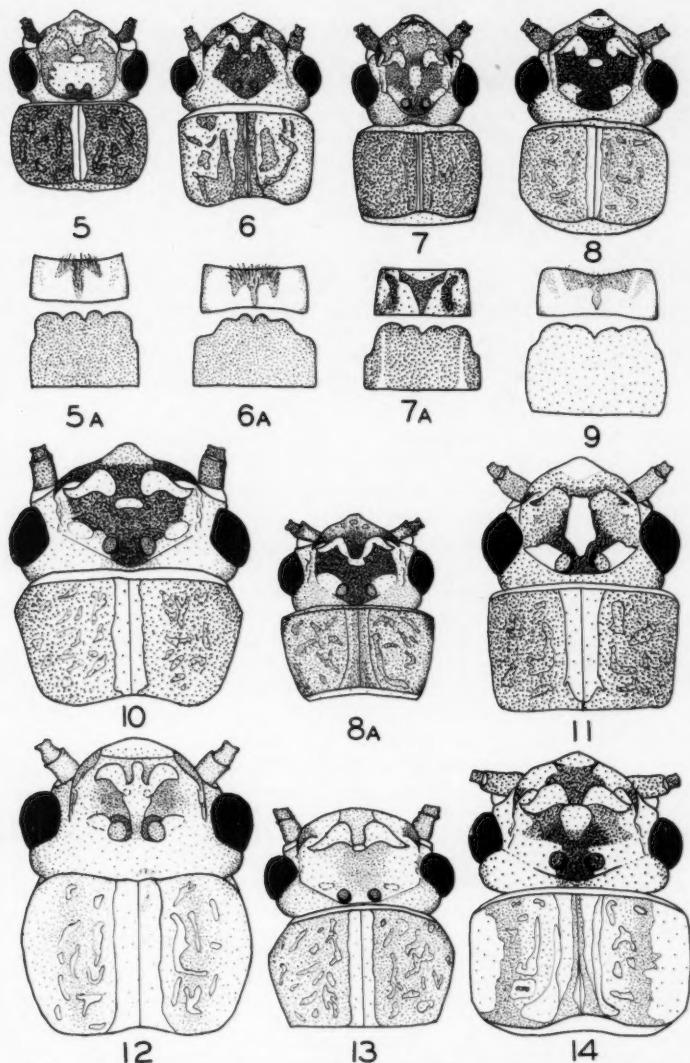
Head yellow and brown in distinctive pattern which is featured by three light spots which form an isosceles triangle anterior and lateral to ocelli, and pair of large light spots anterior to these (outer legs of the M-mark). Dark area is not always so contrasting as in figure. Pronotum brown with many darker brown rugosities, median brown stripe usually dark brown nearly to median suture which may, however, be very narrowly bordered with yellow. Legs brown and yellow; tibiae brown; fore femur brown; middle femur brown with some yellow basally, at most third of length; hind femur almost two-thirds yellow basally; colors sharply delimited on hind femur. Tails yellow to brownish-yellow, sometimes some of segments bicolored (but not in holotype). Wings hyaline, sometimes lightly fumose in males (as in allotype). Costal vein noticeably lighter in color than other veins in female but not in male.

*Female*.—Subgenital plate four-lobed, three notches all rather shallow. Sclerotized area of ninth sternite T-shaped and lightly pigmented with long, modified hairs along lateral borders of T.

*Male*.—With sharply small, conical nail on ninth sternite; smaller and with more sharply defined color pattern than female.

The head and pronotal color pattern characterizes this species.

*Collection Data*.—Female *holotype*, male *allotype*, 2 male and 64 female *paratypes*, Nova Teutonia, Santa Catarina, Brazil, I-56, Fritz Plaumann (holotype, allotype, 10 paratypes CAS, other paratypes to MN, AMNH, BMNH, INHS, USNM, SGJ, JR). Additional *paratypes* with same data as holotype except for dates are as follows: 20-IX-48, ♂ (INHS); X-56, 13 ♀ (SGJ, JR); XI-55, 26 ♀ (SGJ, JR); XI-56, ♂, 3 ♀ (USNM); 5-XI-55, 9 ♀ (SGJ, JR); 6-XI-55, 7 ♀ (SGJ, JR); 7-IX-55, 10 ♀ (SGJ, JR); 8-XI-55, 6 ♀ (SGJ, JR); 9-XI-55, 9 ♀ (CAS).



FIGS. 5-14.—5. *Anacroneuria oculatila*, head and pronotum; 5A, 8th and 9th sternites. 6. *A. novateutonia*, head and pronotum; 6A, 8th and 9th sternites. 7. *A. tinctilamella*, head and pronotum; 7A, 8th and 9th sternites. 8. *A. fuscicosta*, head and pronotum; 8A, head and pronotum of another specimen. 9. *A. aurata*, 8th and 9th sternites. 10. *A. ampla*, head and pronotum. 11. *A. trimacula*, head and pronotum. 12. *A. impensa*, head and pronotum. 13. *A. plaumanni*, head and pronotum. 14. *A. badilinea*, head and pronotum. All figures of *Anacroneuria* based on female specimens.



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## Pigmentation of the Western Spotted Frog, *Rana p. pretiosa*, in Yellowstone Park, Wyoming<sup>1</sup>

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Information on the amount of variation in the pigmentation of *Rana pretiosa* has usually been scanty and based on subjective appraisals of a small number of individuals (Dickerson, 1920; Blanchard, 1921; Patch, 1922; Tanner, 1931; Logier, 1932; Gordon, 1939). All these color descriptions are perfectly valid as generalizations but were not intended to serve as expressions of the variation existing in natural populations.

Color and pattern differences are useful characteristics in attempting to assess inter- and intraspecific relationships but the proper evaluation of pigment variation depends upon adequate understanding of the differences exhibited by the species as a whole, and hence by its component populations.

For example, in her description of the new race *Rana pretiosa luteiventris* Thompson (1913) contrasted, among other characteristics, the yellow ventral pigmentation of the new form with the red or salmon coloring of the nominate subspecies. One may wonder whether such a difference is actually of taxonomic significance or whether ventral coloration varies so greatly over the entire range, or even within adjacent populations, of *Rana pretiosa* as to negate its diagnostic value. Slevin (1928) did not recognize *Rana pretiosa* as a polytypic species and there are others (Stebbins, 1951) who are at least skeptical as regards the validity of *R. p. luteiventris*.

However, the purpose of this study is not to attempt to settle this taxonomic issue but rather to gain some conception of the amount of variation that may be expected in several localized populations of *Rana p. pretiosa* in Yellowstone Park, Wyoming. The expansion of this approach to embrace other populations in other parts of the range of *Rana pretiosa* will eventually permit a decision as to the status of *R. p. luteiventris*.

A similar study of pigmentation has already been carried out in Oregon by Dunlap (1955). His remarks are based largely on preserved material (at least for melanin distribution) with additional notes on ventral color differences based on field observations.

In this study a more restricted geographic area was chosen for

<sup>1</sup> This paper is extracted from the author's doctoral dissertation submitted at the University of California, Berkeley. Part of the preparation of the paper for publication was done while the author was on the staff at Wayne State University.

A contribution from the Museum of Vertebrate Zoology, Berkeley, Calif.



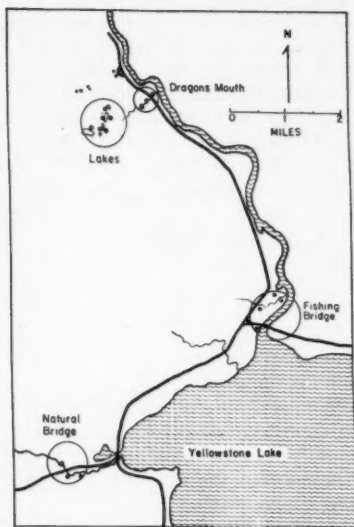


Fig. 1.—Location of 4 populations of *Rana p. pretiosa* in Yellowstone Park, Wyoming, from which samples were drawn. Black circles indicate specific areas sampled.

consideration and an attempt was made to determine the influence, if any, of age, sex, season, or geographic distribution on variation in pigmentation.

*Acknowledgments.*—I wish to acknowledge the role of members of the United States National Park Service in Yellowstone Park, Wyoming, without whose cooperation this study could not have been carried out. Collection of materials was in accordance with the provisions of a Class B permit. Appreciation is also expressed for use of facilities of the Museum of Vertebrate Zoology, and the Department of Zoology, University of California. Finally, it is a pleasure to acknowledge the assistance and direction of Dr. Robert C. Stebbins in the preparation of this manuscript.

#### METHODS

Four populations near the north shore of Yellowstone Lake (Fig. 1) were sampled during 1954 and 1955. Sixty-nine frogs were collected in 1954 and 71 in 1955.

Preserved skins were prepared in the manner outlined by Juszczuk (1952) and mounted with rubber cement on pieces of railroad board of appropriate size. Inasmuch as this technique has not yet been widely used it is felt that a brief discussion of my experience with this method might be of value. During 1954 frogs were killed in weak formalin. This resulted in a small amount of hemorrhage in the dermal capillaries. However, the connective tissue and blood vessels adhering to the skin after its removal were scraped away and the bleeding did not result in discoloration of the dried skin. In 1955 chloretoone was used in place of formalin.

The skins of small frogs (less than 35 mm in length) impose some technical difficulties simply in detaching them originally, and then later in removing them from glass after they have dried. With larger frogs the primary difficulty lies in spreading the wet skin on glass to dry. Folds of skin in the region of the axilla and groin must be arranged as presentably as possible. The central portion of the spread skin tends to bunch in large or fat frogs. Usually drying of the skin results in a disappearance or at least an amelioration of the more unsightly areas. It was found that a slight slit in the tip of the snout and the end of the chin allowed these parts to lie more flatly.

The edges of the skins were smoothed prior to mounting by clipping with small scissors. To avoid possible bias in later analyses only the catalog number of the frog was entered on the face of the card.

The length of each frog (measured immediately after death), its sex (if this could be determined by dissection) and collection data were recorded at the time of dissection and skinning.

Discoloration became apparent in a few skins. The cause of this is not known. The age of the mount and/or the use of rubber cement as an adhesive are possible contributing factors. Why some skins have been affected, and others not, I do not know. Discoloration is apparent ordinarily as a yellowing of the skin, especially the legs. Discolored skins were not used in parts of this study involving analysis of color hue. Irregularities in the shape of skins by tearing or cutting during preparation were cause for rejection of specimens in parts of the study involving analysis of extent and pattern of pigmentation.

To avoid possible discoloration effects of adhesive materials, it would be desirable in the future to affix skins to cardboard by their own moist undersurfaces.

#### VENTRAL PIGMENTATION

The basic pigmentation of the venter is of guanophores which (in otherwise unpigmented individuals) may impart a creamy white to white appearance to the entire undersurface of the body. This immaculate condition is usually exhibited only by juveniles; in older frogs one or both of two other pigments (or pigment types) are almost invariably present to some degree. These are (1) melanin and (2) a lipoid pigment by which the frequently cited yellow, orange, red, or salmon coloration is imparted to ventral portions of the body.

It is with the distribution and occurrence of these last two pigments that this study is concerned.

#### Melanin

Three aspects of the melanin pigmentation of the venter were evaluated: (1) gular area—if not immaculate, displays a mottled, stippled or striped pattern of varying intensity; (2) central portion of the belly—may exhibit the same sort of variation as the chin;

(3) axillae—two triangular areas of melanin may be weakly- to well-defined (see Fig. 4c and 4b). In the same region, in the absence of these "pectoral triangles," two bars running from the axilla anteriorly and medially may be weakly defined or prominent (see Fig. 4a).

In a few instances neither of the last two conditions was discernible in the axillary area and in others it was found that a consistent opinion as to the existing condition could not be formulated.

Melanin patterns on the undersurfaces of the arms and legs, at the periphery of the belly, and in the region of the vent were not analyzed.

A code was designed to enable an evaluation of the above variables:

A—mottled	X—well-defined
B—stippled	Y—weakly-defined
C—striped	0—absent

The numbers 0, 1, 2, 3, and 4 were used to represent five grades of intensity of pigment in a manner similar to that employed by Blair (1943) in analyzing pigments of toads (0 signifying absence of pigment). The melanin pattern and intensity of the gular area could thus be expressed simply as B-2, or A-1, or 0, for example.

It should be stressed that this analysis has been based on features of pigmentation visible to the unaided eye. Dunlap (1955) found that examination with a low power microscope of unpigmented areas where melanin normally occurred revealed melanophores.

Five runs involving 140 skins were made and the results tabulated. When the five evaluations of intensity did not vary from one another by more than one unit (e.g. 1, 1, 2, 2, 1) the values were averaged; if greater disparity obtained the skin was not used in the analysis of the particular aspect of pigmentation involved (*i.e.* 1, 1, 2, 1, 3, would be cause for rejection).

#### GULAR AREA

*Intensity of pigmentation.*—The average intensity value ranged from 0 to 4 and the values for all 140 individuals are plotted by size and sex in Fig. 2. From this distribution several facts may be inferred without resort to statistical analyses:

- 1) gular melanin patterns become evident early in life; certainly during the first full season after transformation if not sooner.
- 2) until the second full season after transformation (at the earliest) the melanin patterns on the chin are faint.
- 3) In later years these patterns may become more intense and their expression is independent of sex; extreme intensities are exhibited by both sexes.
- 4) In a few mature individuals melanistic pigmentation of the chin may not develop. Here again this condition is exhibited in both sexes.

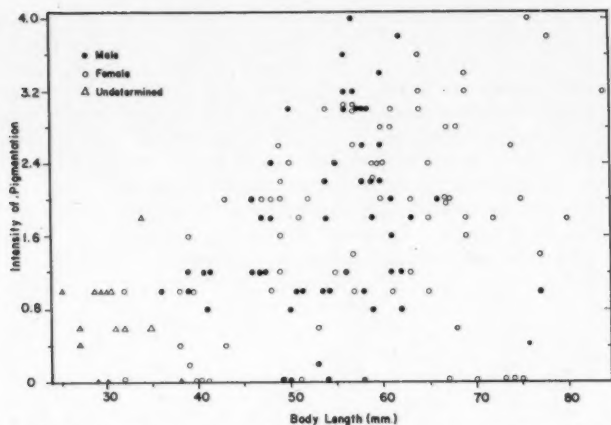


Fig. 2.—Average intensity values for melanin pigmentation of the chin of 140 *Rana p. pretiosa* from Yellowstone Park, Wyoming, indicating size and sex of individuals.

An analysis of 122 frogs representing the four populations revealed no seasonal variation and only one population (Fishing Bridge) seems to differ from any of the others. A statistical test of the four populations was made, revealing that the Fishing Bridge population differs significantly from the three other populations while none of these three differs significantly from the other two ( $\alpha = 0.05$ ).

It seems likely that the low average value for the Fishing Bridge population is a reflection of the relative youth of its members (Table I) and not of environmental or genetic differences.

*Patterns of pigmentation.*—The mottled pattern is by far the most common. Seventy-six of 108 individuals were considered to have mottled chins. Twelve had stippled chins and only two exhibited striped chins. Fifteen frogs displayed conditions intermediate to stippled and mottled, and three were intermediate to striped and mottled.

TABLE I.—Intensity of gular pigmentation of *Rana p. pretiosa* in Yellowstone Park, Wyoming

	Dragon's Mouth	Natural Bridge	Fishing Bridge	Lakes
Number of individuals	41	35	23	23
Average body length (mm)	50.8	54.0	44.5	63.4
Average melanin intensity	1.80	1.87	1.26	1.77
Variance	1.46	0.85	1.07	1.05

TABLE II.—Melanin pigmentation of the axillae of *Rana p. pretiosa* from Yellowstone Park, Wyoming. An intensity value of 0 denotes absence of melanin, of 1.0, maximal pigmentation

Axillar pigmentation	Both pectoral bar and triangle absent	Pectoral triangle	Pectoral bar	Pectoral triangle	Pectoral bar	Pectoral triangle	Pectoral bar	Total number of individuals
Body length (mm)								
(Intensity of pigmentation)	0	0.1-0.4		0.5-0.7		0.8-1.0		
25 - 35	6	0	2	0	6	0	2	16
36 - 45	5	0	1	0	6	0	4	16
46 - 55	2	1	2	2	8	1	13	29
56 - 65	0	0	0	13	2	16	3	34
66 - 75	1	1	0	7	0	9	0	18
76 - 85	0	0	0	0	1	4	0	5
Totals	14	2	5	22	23	30	22	118

## AXILLAE

The presence of triangular pigmented areas in the axillae is evidently an adult characteristic (Table II). In 118 individuals where the pattern of pigmentation in the axilla could be defined this characteristic was only apparent in frogs 50 mm or more in length. Of 57 frogs, 56 mm or more in body length, 50 (87.7 percent) exhibited more or less well-defined pectoral triangles.

There is no significant difference between the sexes in the degree of expression of the pectoral triangle.

Further analysis indicates that there are neither seasonal variations nor differences between the populations except those which would be expected in view of the comparative sizes of the frogs making up the samples.

Evidently the pectoral bar is a juvenal precursor of the pectoral triangle. This characteristic does not ordinarily persist in older frogs but there seems to be considerable variation in the age at which it is first expressed (Table II). There is certainly a suggestion that the bar is most strongly defined in frogs ranging from about 47 to 57 mm in length, or at an age immediately prior to the manifestation of the pectoral triangle. There are neither seasonal variations nor differences between the populations with respect to this characteristic.

## BELLY

*Intensity of pigmentation.*—The average intensity value ranged from 0 to 3.4 in 138 frogs analyzed. These values are plotted in

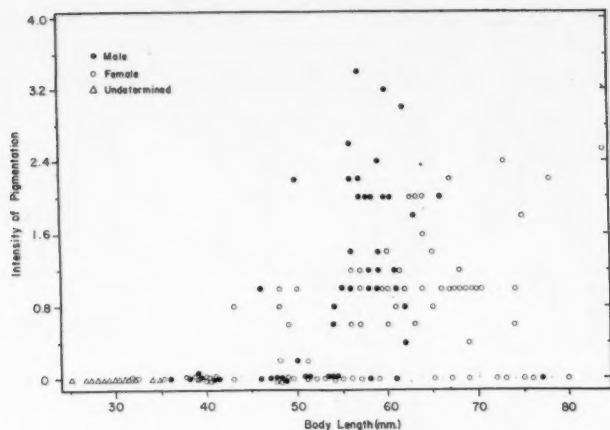


Fig. 3.—Average intensity values for melanin pigmentation of the belly of 138 *Rana p. pretiosa* from Yellowstone Park, Wyoming, indicating size and sex of individuals.

Fig. 3 from which certain inferences may be drawn. Melanin patterns on the belly do not appear until about three years after transformation at the earliest. Actually the expression of these patterns is not manifested until several years later in the majority of individuals. With greater age the belly may become more intensely pigmented, but an appreciable number of frogs apparently never develop this type of pigmentation. An analysis of 107 frogs, 46 mm or more in length, was carried out and the results are presented in Table III.

Apparently there is no significant difference between the sexes.

An analysis of the four populations was made; the Fishing Bridge population differed significantly from the other three. As in the case of gular melanism this difference is undoubtedly associated with the age difference in the samples. No seasonal variation seems to occur.

*Patterns of pigmentation.*—Of 75 frogs with melanin pigmented bellies, 68 exhibited a stippled pattern. Three were striped, one mottled, and three others seemed intermediate to stippled and mottled. Representative patterns are illustrated in Fig. 4.

TABLE III.—Intensity of melanin pigmentation of the belly of male and female *Rana p. pretiosa* from Yellowstone Park, Wyoming.

	N	Range of intensity values	Mean	Variance	Standard error
Males	44	0 - 3.4	1.13	1.06	0.16
Females	63	0 - 2.6	0.78	0.71	0.09



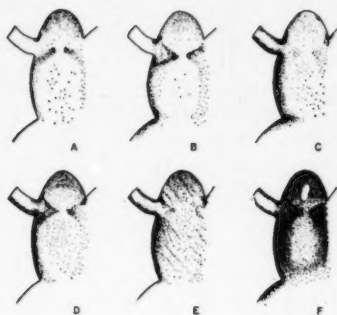


Fig. 4.—Representative patterns and intensities of ventral melanin pigmentation of 6 *Rana p. pretiosa* from Yellowstone Park, Wyoming. A—Female; chin A-2, belly B-1, pectoral bar well-defined. B—Female; chin B-1.8, belly 0, pectoral triangle well-defined. C—Female; chin A-1.4, belly B-1, pectoral triangle weakly-defined. D—Male; chin A-3, belly B-2.2, pectoral triangle well-defined. E—Male; chin C-3.2, belly C-2.2, axilla indeterminate. F—Male; chin A-4, belly B-3.4, pectoral triangle well-defined.

### Lipoid Pigment

The orange pigmentation of the venter is most evident on the belly, but may also occur on the arms, chin, thighs, shanks and feet. Because of the manner in which the skins were prepared, it was not possible to analyze the variation in pigmentation of the feet.

The anterior limit of the belly was arbitrarily defined by a line running from the axilla to the hole representing the original location of the missing arm. That portion of the skin anterior to this line was considered the chin. The posterior limit of the belly was defined by an unpigmented arc lying between the pigmented area of the belly and the more posterior pigmented areas.

The skins of 140 frogs examined and 24 exhibited no lipoid pigmentation. Of these 24 all but two were juveniles or subadults ranging from 25 to 41 mm in length. Of the two adults one was the largest male taken in the entire sample (77 mm in length) and the other was a female 54 mm long.

### CHIN

Ten frogs (of 140) exhibited some pigmentation of the chin. All of these were adults and, with one exception, females. Except for the smallest of the nine females, all these frogs were large adults ranging from 60 to 76 mm in length.

### EXTREMITIES

The occurrence and quality of pigmentation of these areas have been analyzed jointly and the results are tabulated in Fig. 5. Estimates of intensity are subjective and based on a single inspection. Hence only very general conclusions are justified, but the critical points are clear.

It is evident that the earliest expression of lipoid pigmentation is on the shanks. Of 116 frogs only 2 (a 32 mm female and a 41 mm male) lacked pigmentation of this area and exhibited it elsewhere. In

both of these frogs the thighs showed a trace of pigment.

Full intensity of shank pigmentation occurs usually by the time the size of 52 mm is attained.

The development of the pigmentation of the thighs and arms seems roughly comparable and is characterized by the persistence of the unpigmented or lightly pigmented condition in a larger percentage of individuals, and perhaps by a slight retardation in time of full expression. These relationships are expressed quantitatively in Table IV.

#### BELLY

Because the lipid pigmentation of the belly area usually constitutes the major ventral coloration, and because of the presumed taxonomic significance of this characteristic, a special analysis of this feature of pigmentation was performed.

*Hue.*—The color of the lipid pigmentation of *Rana p. pretiosa* has been variously described as salmon-red, red, rich salmon, etc., and authors who have encountered orange, orange-red, or yellow pigmented individuals have been prone to consider them *Rana p. luteiventris* (Gordon, 1939; Dunlap, 1955).

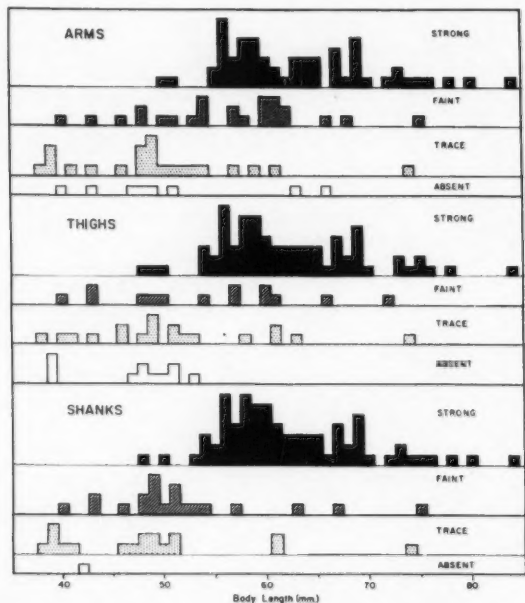


Fig. 5.—Lipoid pigmentation of the extremities of 116 *Rana p. pretiosa* from Yellowstone Park, Wyoming. Each square represents one individual.

TABLE IV.—Lipoid pigmentation of the extremities in relation to body size in 116 *Rana p. pretiosa* from Yellowstone Park, Wyoming

	Normal	Intensity of pigmentation	
		Faint or trace	Absent
Shanks			
32-52 mm	2 (6.0%)	29 (88.0%)	2 (6.0%)
53 mm+	74 (89.2%)	9 (10.8%)	0
Arms			
38-54 mm	2 (5.2%)	30 (76.9%)	7 (17.9%)
55 mm+	57 (74.0%)	18 (23.4%)	2 (2.6%)
Thighs			
32-53 mm	3 (8.6%)	21 (60.0%)	11 (31.4%)
54 mm+	68 (84.0%)	13 (16.0%)	0

Aside from the unfortunate ambiguity associated with such color designations, it is likely that this criterion for separation of the races (which seems satisfactory in Oregon) will not prove adequate in all other areas. For example near Salt Lake City, Utah, what is considered to be *Rana p. pretiosa* is definitely yellowish-orange ventrally and in parts of western Wyoming, where I have observed *Rana p. pretiosa*, the lipoid pigmentation is better described as orange than red.

In an attempt to analyze the variation and color quality in Yellowstone Park populations, 47 skins (12 males and 35 females) were selected. Skins with heavy melanin suffusions on the belly were not used and this rendered some of the larger males unsuitable for study. The color of the belly was compared with color plates in Maerz and Paul (1950).

It was found that within practical limits all lipoid pigmentation could be matched on Plate 9 of Maerz and Paul. More specifically, the total variation was included within a rectangle of 30 squares (A-E, 4-9 inclusive). This area includes the following color names: Peach (A5), Burnous (C4), Capucine Buff (E5), Trianon (B7), Honeydew (B8), and Ceres (C8).

*Extent.*—It was felt that some quantitative expression (in terms of area) of the pigmentation should be derived and that these values should be directly comparable. Obviously the comparison of absolute values (which would be influenced by the size of the specimen involved) would not be significant. Furthermore, because of the manner in which the skins were prepared, variations in the extent of the "total belly area" could have been introduced depending on the location of the cut along the side of the body. Hence, some method for calculating the "belly area" of a frog as a function of its body length seemed advisable. The belly areas of four 56 mm frogs were measured with a planimeter and the four values averaged to obtain a mean of 7.58 square centimeters. The area of the belly varies as the product of the linear body dimensions. Assuming that body length and width increase at the same rate, the total belly area can be

approximated as a linear function of the square of the body length ( $5.6^2 = 31.36$ ).

To check this assumption the belly areas of 49 additional frogs were determined with a planimeter and these values plotted against the squares of the body lengths of the same frogs. On the same graph a line was drawn representing the relationship of belly area to square of body length using the formula:  $\text{Area} = 0.25 (\text{body length})^2$ . The agreement of the measured values and the line representing the artificially derived values was considered close enough to justify the computation of belly areas by means of the above formula.

Having established a basis for the determination of the "total belly area" it was now possible to measure the actual pigmented portion of the belly and calculate the percent of the belly area pigmented. Nine frogs with scant pigmentation were analyzed visually by comparison with a standard which had a measured pigmented area of less than 0.1 square centimeter. On six skins the pigment was somewhat scattered and in these cases the major area was outlined with enough unpigmented area included to compensate for omitted pigmented areas.

The percent of belly pigmented in 81 frogs was calculated and the values are represented graphically in Fig. 6.

A statistical analysis (involving 45 females and 26 males) employing the standard error of the mean was performed. While the difference between the sexes is not significant at the 5 percent level, it is at the 10 percent level (Table V). The variances of the male and female samples differ significantly. I believe it is safe to conclude that extensive pigmentation of the belly, i.e., 30 percent or more, is a characteristic expressed predominantly in larger females. It is also likely that belly pigmentation develops in females at an earlier age (i.e., at a size of approximately 40 mm) than in males. The smallest males exhibiting belly pigmentation were 50 mm in length.

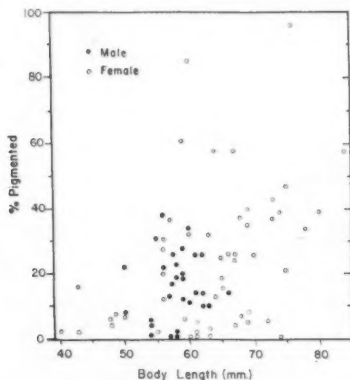


Fig. 6.—Percent of total belly area with lipid pigmentation in 81 *Rana p. pretiosa* from Yellowstone Park, Wyoming.

TABLE V.—Percent of total belly area with lipid pigmentation in female and male *Rana p. pretiosa* from Yellowstone Park, Wyoming

	N	Range	Mean	Variance	Standard error
Males	26	4.3 - 38.3	18.8	9.2	1.8
Females	45	1.2 - 95.4	27.7	23.4	3.5

There do not seem to be any differences in extent of pigmentation associated with time of season, or with the four different populations.

*Pattern.*—Both Dickerson (1920) and Patch (1922) describe the salmon-red ventral markings on the belly of *Rana p. pretiosa* as U-shaped. The pattern of lipid pigmentation on the belly of 82 skins was examined in order to determine the frequency of this characteristic. Four arbitrary categories were established and the skins were assigned on the basis of a single inspection. The results are summarized in Table VI.

Nine skins representing each of the above categories are displayed in Fig. 7.

That the development of a recognizable U-shaped pattern may depend to some extent on age is suggested by the average size of the frogs making up the first three categories. The pigment pattern on many of the skins assigned to the third category was such that a U-shaped distribution could develop by appropriate additions to the existing patterns (e.g., Fig. 7a).

#### DORSAL PIGMENTATION

##### GROUND COLOR

General agreement among investigators seems to exist as to the ground color of the dorsum of *Rana p. pretiosa*. The range of variation suggested is probably no more than that which might be exhibited by a single individual from any population under varying environmental conditions. Consequently there seems to be little value

TABLE VI.—Configuration of lipid pigment on the belly of *Rana p. pretiosa* from Yellowstone Park, Wyoming

	Definitely U-shaped	Pattern faint, incomplete, or irregular, but discernibly U-shaped	Irregular spots or suffusions (usually located posteriorly)	Other
Number	22	28	27	5
Range in size of frogs (mm)	55-78	43-84	40-74	
Mean size	64.6	62.4	56.8	

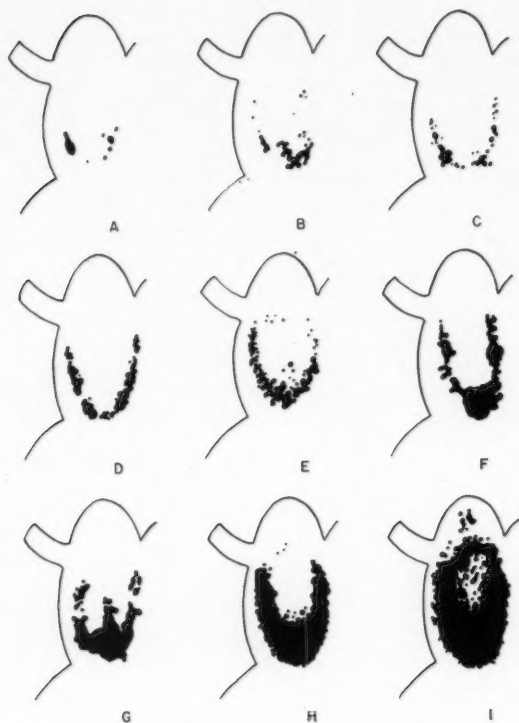


Fig. 7.—Pattern of lipoid pigmentation of the belly in 9 *Rana p. pretiosa* from Yellowstone Park, Wyoming.

in attempting to specifically define anything more than the approximate limits of variation.

On the basis of examination of 30 skins and comparison with color plates in Maerz and Paul (1950), it may be stated that the ground color of all skins which can be matched is best duplicated on Plate 16 by the following squares: E 3-7, H 2-7, J 3-8, and L 5-8. Sagebrush green, Beetle, and Bronze Green + are specific colors listed among this array. Skins which could not be matched were invariably too black.

#### DORSAL SPOTTING

The dorsal spots of *Rana p. pretiosa* have been variously described by Dickerson (1920), Patch (1922), Tanner (1931), Logier (1932),



Gordon (1939), and Dunlap (1955). All agree as to the irregular outline of the spots. The Yellowstone populations are typical in this respect.

The only really serious analysis of the character of the spots has been that of Dunlap (1955) who concluded that *Rana p. pretiosa* could be effectively separated (about 96 percent) from *Rana cascadae* on the basis of the appearance of the dorsal spots. Two characteristics were considered highly diagnostic by Dunlap—the margin of the spots (distinct in *Rana cascadae* and indistinct in *R. pretiosa*) and the light centers of the spots of *R. pretiosa* as opposed to the solid spots of *R. cascadae*.

An examination of 113 skins of *Rana p. pretiosa* from Yellowstone Park was made. The skins were assigned to one of three categories related to the nature of the dorsal spots. In 55 skins the majority of the spots exhibited continuous margins and light centers, in 42 there were light centers but discontinuous margins, and in 16 the spots lacked light centers.

It may be seen that the dorsal spots of all but 16 skins (85.8 percent) possessed light centers but that there is considerable variation

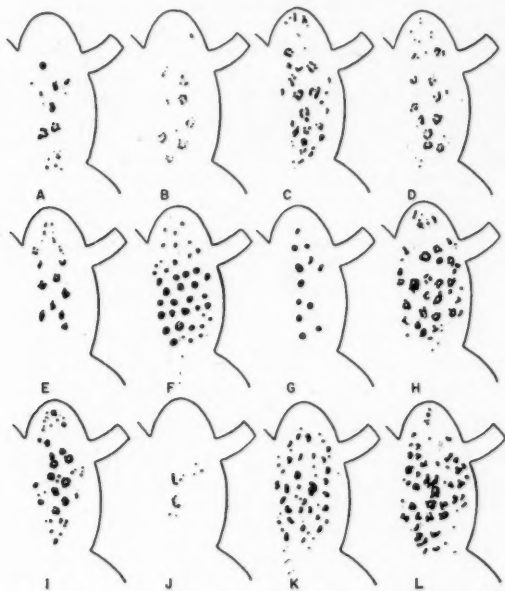


Fig. 8.—Dorsal spotting of 12 *Rana p. pretiosa* from Yellowstone Park, Wyoming.

within the limits of this broad characteristic. Discontinuous margins (Fig. 8 a, b, c, d) are almost as common as continuous margins (Fig. 8 e, f, g, h, i). The light centers vary from evident (Fig. 8 g) to barely discernible (Fig. 8 f). About 14 percent of the skins exhibited spots without light centers, or which differed in some other manner from the first two categories (Fig. 8 j, k, l).

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## A Contribution on the Life History of the Collared Peccary in Arizona<sup>1</sup>

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The collared peccary, *Pecari tajacu sonoriensis* (Mearns) is a common inhabitant of central and southeastern Arizona. It is found from about 2,000 feet above sea level in the Sonoran desert of southeastern Arizona to an altitude of over 6,500 feet above sea level in the higher ranges (Knipe, 1957).

Between September, 1955 and January, 1957, I conducted research on the techniques of trapping, tagging, and transplanting the collared peccary. While carrying out this research work miscellaneous information on the life history of the collared peccary was obtained.

*Study area.*—Most of the field work was conducted in the Tucson Mountains, located about six miles west of Tucson in Pima County, Arizona. Elevations range from about 2,200 feet above sea level at the lower elevations to 4,677 feet above sea level on Wasson Peak, the highest point in the Tucson range. The terrain is rugged in the higher elevations around 3,000 feet above sea level with numerous rocky outcrops scattered throughout the higher peaks. Below the foothills, the terrain levels out into sandy plains.

Climatic conditions in the study area consist of high temperature, high evaporation, and low annual rainfall. The greater part of the annual precipitation usually comes as summer thunderstorms which are of short duration. The winter rains, unlike the sudden summer downpours, may last several hours with a slow-soaking precipitation that percolates into the soil and is retained (U. S. Dept. of Agriculture, 1941).

The study area lies wholly within the Sonoran Desert (Shreve, 1951). The principle feature of this area is the great variety of cacti which grow in association with the creosote-bush (*Larrea tridentata*), bur-sage (*Franseria deltoidea*), mesquite (*Prosopis juliflora*), palo verde (*Cercidium microphyllum*), and ironwood (*Olneya tesota*). Saguaro (*Carnegiea gigantea*) is abundant throughout most of the area and in places forms dense stands. Cholla and prickly pear (*Opuntia* sp.) are less striking but even more abundant than saguaro. The hedgehog cactus (*Echinocereus* sp.), barrel cactus (*Ferocactus wislizeni*), and fishhook cactus (*Mammillaria* sp.) are

<sup>1</sup> Contribution from the Arizona Cooperative Wildlife Research Unit: University of Arizona, Arizona Game and Fish Commission, U. S. Fish and Wildlife Service, and the Wildlife Management Institute.

also common. The fruits of each, in addition to the roots and fleshy pads of prickly pear, are eaten by wildlife.

Most of the year the animals that require free water depend on man-made waterholes located throughout the area. In the western portion of the study area, several wells and tanks supply the animals with water. The eastern portion is largely settled by residences and guest ranches, many of which provide permanent water for the several species of animals present.

*Breeding.*—Breeding in peccary herds appears to take place in all months of the year. McCulloch (1955) records a breeding observation in southern Arizona during February. Jennings and Harris (1953) report mating activity in Texas in December.

In the present study, I observed mating in two members of a herd of five peccaries in the Tucson Mountains on August 16, 1956. The three non-mating members were between 75 and 100 yards away, and appeared to take no interest in the mating pair. During the ten minutes that this behavior was under observation, the male mounted the female five times, and stayed mounted for an average of one minute.

Mating activity was noted in a herd of eleven adults and four young peccaries on December 10, 1956. Two adults from this herd were observed about fifty yards from the main herd at 3:40 p.m.; the male mounted the female two times for about thirty seconds each time. Two separate pairs from this herd were observed mating at 4:15 p.m. In all three observations, the mating took place only a short distance from other members of the herd who appeared to take no interest in the mating activity.

Mating was observed again in the above herd on December 23, 1956 at 12:05 p.m. In one instance, mating activity lasted for fifteen minutes, during which a total of eight mounts were made by the male. The male stayed mounted about fifty seconds each time, and the longest mount was two minutes. A second pair was observed breeding at 12:30 p.m. The male mounted the female four times in a period of ten minutes. The fourth mount was over three minutes in length; successful copulation appeared to have taken place this last time, as withdrawal of the penis from the vagina was observed. One adult approached the mating pair and was vigorously chased away by the breeding male. A third pair was observed breeding at 12:48 p.m. A pair of twins about two months old followed the female. During the time the male was mounted, the twins, which were about twenty yards away, ran to the female and tried to nurse. This disturbance caused the male to dismount and run off about fifty yards. After the disturbance, no other mating was observed in this pair.

On December 26, 1956, a tagged adult male and female from the above mentioned herd were observed mating at 3:36 p.m. Only two mounts were made by the male; the pair then joined the other herd members and were last observed walking over a ridge.

*Month of birth.*—Knipe (1957) states that the peak of production

in Arizona peccary herds is reached from midsummer through late fall.

From field observation in the present study, 55 birth records were obtained on Arizona peccaries. The following list gives these records by months:

January—0	July—24
February—5	August—10
March—1	September— 1
April—0	October— 1
May—2	November— 2
June—7	December— 2

Seventy-four percent of these young were born during the summer months of June, July, and August. In most of the observations, the young were caught when only a few days old, and in others, the teeth eruption pattern was used to arrive at an estimated age (Kirkpatrick, 1957).

*Litter size.*—Jennings and Harris (1953) give the litter size as one (a frequent occurrence) to four (rarely) in Texas. Seven pregnant females collected by these two workers contained an average of 1.28 embryos. Halloran (1945) reported five fetuses from an Arizona peccary.

Knipe (1957), from 45 field observations on females with young, recorded 25 females with 1 young, 17 with 2 young, and 1 with 3 young, for an average of 1.44 young per female. In the present study, 16 females were observed with 1 young, 7 with 2 young, and 3 with 3 young, an average of 1.81 young per female.

Observations in the present study and those of other workers indicate that the average litter size is about 1.5.

*Mammæ.*—Thirty adult female peccaries were trapped and examined. The number of functional mammæ was four in every instance. In addition, four rudimentary mammæ were found anterior to the functional four. These four pairs of mammary glands are distributed ventrally from rear to front as follows: one pair in the inguinal regional (functional); a post abdominal pair (functional); and two pectoral pairs (rudimentary).

Jennings and Harris (1953) report finding 4 teats in 28 females collected, and Knipe (1957) also reports 4 mammæ in Arizona peccaries. Apparently, these three workers were referring to the four functional mammæ. Wislocki (1931), however, reported finding only two mammæ on one female examined.

*Size and body weight.*—Two trapped wild sows each gave birth to a litter of three young on July 15 and July 18, 1956. Weights of 4 of these 6 young peccaries were obtained before they were two days old. The average was one pound, extremes, 0.7 and 1.5 pounds.

A pair of twins captured on August 4, 1956, in the Tucson Mountains, weighed one pound each. Their age was estimated at two days, and both still had their umbilical cord attached.

TABLE I.—Average weight in pounds of adult peccaries

Sex	Av. Wt.	Variation	No. Examined
Female	45.7	35-54	31
Male	43.8	35-51	17

Weights and measurements were taken from forty-eight adult peccaries captured in the Tucson Mountains (Tables I and II).

*Growth.*—A litter of three peccaries was born on October 5, 1956 at the Arizona-Sonora Desert Museum, 16 miles west of Tucson. Two of the litter survived and were observed at weekly intervals (Fig. 1). The reddish-brown pelage of the two young peccaries began to be replaced by adult pelage at one month; and the two young stayed in a transition stage between reddish-brown juvenile pelage and the grizzled-gray pelage of the adults until they were between three and four months old. At four months, the two young had completely acquired the adult pelage. The last areas on the young to lose the reddish-brown bristles were the flanks and head regions. In adults, the bristle-like hairs may be over 160 mm in length around the scent gland region and along the back. The dorsal row of bristles normally lies flat along the back but may be raised when the peccary is alarmed.

The two captive peccaries nursed heavily until they were a month old, at which time they began taking solid foods (Walker, 1956). They were weaned when between three and four months old. Based on field observations, wild sows weaned their young when they were between two and three months of age.

*Protective adaptations.*—Young peccaries were able to follow their mothers within a few hours after birth. They appeared to inherit the temperament of their parents, for they exhibited at an age of one day the same defensive behavior as the adults, and would slash at my hand with their sharp canine teeth when I attempted to handle them.

Ten young peccaries (from a few hours to two days old) had four well-developed canine teeth and the third lower incisors present, a total of six teeth each. The canine teeth of adults appear to be used mainly as weapons of defense. In watching peccaries eat prickly pear, I observed that the incisor teeth were used for biting, and the premolars and molar teeth did the crushing and chewing. The canines were used little. The length of the canine teeth from the gum line

TABLE II.—Measurements in millimeters of adult peccaries

Sex	TL* Av.	Variation	No. Exam.	HF** Av.	Variation	No. Exam.	Ear Av.	Variation	No. Exam.
Female	848	812-875	5	192	175-205	14	90	80-96	13
Male	850	—	1	190	175-200	10	89	59-94	11

\*TL=total length.

\*\*HF=hind foot.



measured to 41 mm in some mature adults. Three boxer dogs known to have had encounters with peccaries in the Tucson Mountains were examined. Healed scars up to four inches were evident on the neck and shoulders. The owner informed me that peccaries had inflicted these wounds on the dogs.

Young peccaries stay close to their mother during the first two or three months after birth. I usually found the young peccaries only a few feet away from the sow, while the sow was moving, feeding, or lying down. Undoubtedly, this close attachment during the early months of life has survival value for the young. Maternal attachment appears to be more developed in the does of antelope and deer than in the mother peccaries. I have captured and tagged young peccaries in the field, only to have the sow run away and not return. For example, a one month old peccary was captured on October 5, 1956 out of a herd of five adults and two young. I approached to within



Fig. 1.—Pair of peccaries two weeks old nursing at the Arizona-Sonora Desert Museum.

ten yards of the herd before they detected me; all five of the adults fled over a ridge some 500 yards away. I located one of the young lying on its belly adjacent to a bush. Although it squealed loudly upon being captured, none of the adults came back during the next two hours. In tagging studies on antelope and deer in Nevada, I found that the does normally stayed within 300 to 400 yards of their young while they are being tagged; a few hours after withdrawal of the tagging crew, the does returned to the area where their young were released.

In only one instance did a mother peccary stay near the young while it was being handled. The young animal was captured in the Tucson Mountains on December 2, 1955 from a herd of six adults and one subadult. All members of the herd fled, when they detected me in the immediate area, except one adult, apparently the mother. This adult circled about fifty yards away during the ten minutes that the young was tagged and examined. The young peccary was about one day old; its umbilical cord was still attached.

*Parental relations.*—The rearing of the young is left to the sow. It is a frequent occurrence in a herd to see the sow and young feeding by themselves. A female peccary with young appears to be less socially dependent on the herd than do barren females. Males appear to take slight interest in rearing the young. Young peccaries apparently never leave the herd, for young of all age classes have been trapped in the Tucson Mountain herds.

A wild, trapped female in captivity gave birth to a litter of three on the morning of June 15, 1956. One was apparently born dead, and the remaining two were found dead several hours later with teeth marks on them. It appears that the five females in the pen killed the young; however, the adults made no attempt to eat the dead young. The five females were trapped only two days before the litter was born, and the excitement of being trapped and placed in close confinement probably created an abnormal situation, which caused the females to kill the young. Domestic pigs have been known to kill their young when placed in close confinement.

*Enemies of young.*—Jennings and Harris (1953) believe that the coyote, wildcats, and lions take a heavy toll of peccary young in Texas. Knipe (1957) listed the coyote and bobcat as major predators on young peccaries in Arizona. Murie (1951) found peccary remains in only 3 of 3,981 coyote scats gathered on the San Carlos Indian Reservation in Arizona; he did not indicate whether the remains were of young or adult peccaries.

A herd of eleven adults and five young were observed weekly from November 12, 1955 to June 10, 1956. One of the five young was killed during trapping operations. Remains of a second young, which had been marked previously with red paint, were found in an arroyo bed. Fresh blood and scattered debris in the area indicated that an unknown predator had killed this animal. The three remaining young were observed with the herd on November 29, 1955, but were

TABLE III.—Sex and age data on three peccary herds.

Herd No.	Size	Adult Females	Adult Males	Immature Females	Immature Males
1	6	1	3	2	0
2	15	6	3	4	2
3	7	4	1	1	1
Totals	29	11	7	7	3

not with the herd on April 29, 1956, or on June 10, 1956, when the entire herd was captured in a corral trap. Between November and April, these three remaining young were lost to unknown causes. This herd did not increase during the seven months.

Another young peccary was observed in a herd of seven animals on December 5, 1955. It was captured by me, and its age was estimated at between one and two days. This herd was observed again on February 3, 1956, and the young peccary was absent from the herd at that time and in later observations. Its loss from the herd occurred sometime between December and February.

Out of four young peccary carcasses found in the field, two were attributed to unknown causes, one to an unknown predator, and one was a road kill.

**Herd composition.**—During trapping operations in the Tucson Mountains, complete herd compositions were obtained on three herds. Table III gives the sex and age on these three herds. Herd 1 had a predominance of adult males over adult females, whereas Herds 2 and 3 had a predominance of females in this class. Additional herds should be studied before any conclusions on composition can be drawn.

**Shelters.**—Miller (1930) found peccaries in burrows and in excavations of the giant armadillo in Brazil, where they sought refuge whenever possible. Burrows were always located at the roots of a fallen tree, or similar spot, where a natural cavity occurred that could be enlarged with the minimum effort. Jennings and Harris (1953) found bedding grounds more frequently at the bases of guayacan bushes (*Porlieria angustifolia*) than under other brush in Texas.

In Arizona, peccaries have been found living in both natural and artificial caves; piles of excrement over an inch deep in many of the caves indicate their use. The bases of boulders were found to be favorite bedding sites. Beds were also located commonly under a mesquite (*Prosopis*), palo verde (*Cercidium*), or ironwood (*Olnya*) tree on brushy, sloping arroyo banks. The factors that appear to govern the selection of a bedding or resting site in the Tucson Mountains are protection from heat in summer and shelter from the winter cold. I found no particular habitat preferred as bedding or resting sites; availability of sites appeared to be the determining factor.

**Disposition and temperament.**—In contrast to deer and antelope, which are often considered animals with nervous dispositions (Elder, 1956; Buechner, 1950), the peccary is a calm animal. A herd of 15 was kept under observation for six hours in December, 1956. In the

herd fed during the entire time, and only occasionally would an animal stop eating to listen and observe. Elder (1956) gives a vivid account of male deer and peccary behavior around a man-made waterhole in the Tucson Mountains. In general, the behavior of deer upon approaching a waterhole was characterized by caution and hesitation, whereas peccaries headed for the water tank and milled around the area rooting and feeding, sometimes staying as long as 45 minutes in the area before leaving. The peccary's calm disposition does not leave him devoid of curiosity. On two occasions, involving a single adult, and a pair of adults, peccaries left their herds to approach within 15 feet of me. The animals grunted frequently and showed fear by the upraised hairs along the back. Their curiosity apparently satisfied, they moved back to the feeding herd about one hundred yards away.

I have never observed adult peccaries playing. Quarrels and fights of short duration are common, especially while the animals are together at a waterhole or bedding site. However, herds of ten to fifteen animals have been seen feeding and bedding together for several hours at a time with little friction. Young peccaries under two months old were commonly observed playing together at the Arizona-Sonora Desert Museum.

*Old age.*—The peccary is a highly sociable and gregarious mammal, and it is usual to see between 7 to 15 animals together in one herd. Some individual males, however, are seen living alone, and are often referred to as a *solitario* in contrast to the majority who live in herds. Two old males were trapped from a herd of 15 (3 adult males, 6 adult females, and 6 young) on November 11, 1955. In later observations on December 6 and 8, 1955, I found these two old males together. A search of the area failed to find the other members of the herd. On February 17, 1956, the same two males were killed by archers during the hunting season, while apparently still living apart from the herd. The other adult male in the herd was a mature animal that was observed with the herd on all later observations. Whether the two old males were separated from the herd by a social conflict with the younger male, or merely failed to rejoin the herd upon release, is not known.

*Scent gland.*—Both sexes have a scent gland. It is situated on the back about eight inches from the base of the tail. Seton (1929) in referring to musk-glands states, "These musk-glands are usually developed as a part of a signal system, as in deer, antelope, and wolves; and there can be no doubt as such they serve the peccary."

In breeding activity, the mating behavior of the male between mounts consisted of biting the female's ears and rubbing her scent gland with his nose. Undoubtedly, this behavior has some part in stimulating the female to receptivity.

Adult animals in the field and in captivity were observed rubbing each other's scent gland (Fig. 2). This behavior was observed commonly when two adults came in contact with each other along a trail,

feeding, or standing in a herd. It consisted of side to side contact with vigorous rubbing of each other's scent gland, from about three to ten seconds. The rubbing behavior was not reciprocal in all instances. The side of the lower jaw and head, just below the eye, was used for rubbing the glands. This behavior begins at an early age. Two-month old peccaries at the Arizona-Sonora Desert Museum were observed rubbing scent glands with adults. The behavior appears to be a herd-member recognition factor, for it has been observed in the field only in animals from the same herd. Further studies of the recognition factor are needed before definite conclusions can be reached.

The musk from this gland is apparently used as an alarm signal, as well as a means of keeping the herd together. When a peccary

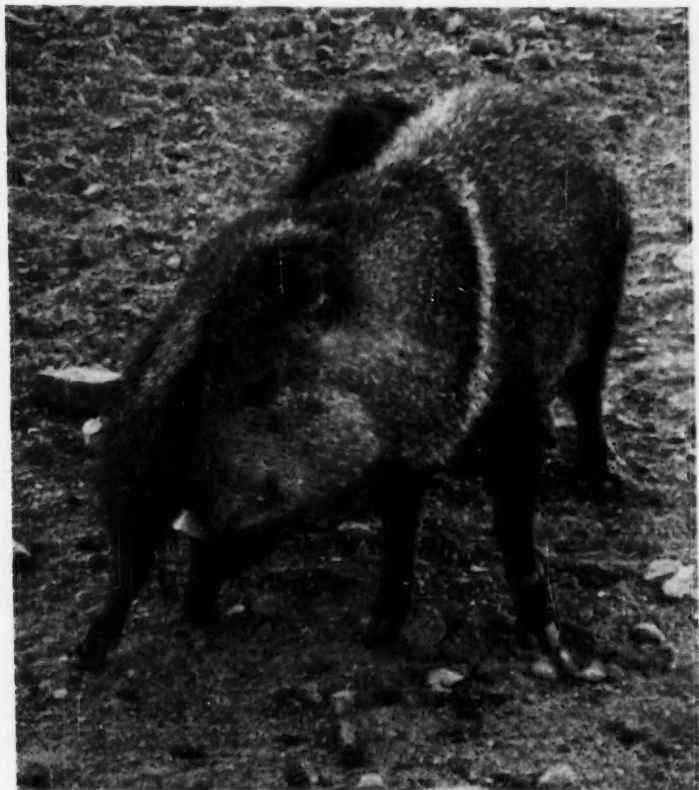


Fig. 2.—Adult peccaries rubbing scent glands.

herd is alarmed, a wave of musk may be left behind by the retreating members; this probably serves as a danger signal to other peccaries in the area. The musk may be forcibly ejected from the gland. In one instance, the musk was ejected for about one foot by an excited peccary at the Arizona-Sonora Desert Museum.

*Intercommunication.*—Communication between adult members of a herd is audible under ordinary conditions only at close range. While watching a herd of 15 animals feeding over an area of about 100 yards diameter, I was able to hear the communicating grunts made by the adult peccaries. I was standing in the center of the herd less than 25 yards from the nearest member. Herd members that strayed from the immediate area while feeding tried to regain contact with the herd by emitting a low grunt. If a reply was not received, the stray animal gave a louder grunt in shorter frequencies, until vocal contact was made with the other members. This grunt is heard continuously while a herd is feeding, and is described by Enders (1930) as the contented grunt of feeding. The sound of the young peccaries, in contrast, can be heard at a greater distance than the adult's grunt. The young peccaries' communicating signal may be described as a sharp squeal. This squeal is heard when the young peccary is separated from its mother, in many instances by only a few yards, or when it wishes to nurse. Several times peccary herds were located in the field by listening for the young animal's voice. In one instance, I located a herd over a quarter mile away in a canyon by this method.

When alarmed, either sex may give a loud "woof" as the alert signal. This signal alone does not appear to alarm the entire herd; however, if the signal is accompanied by running of some of the herd members, the entire herd normally scatters in all directions. Accompanying this excitement, the peccaries' scent glands give off a characteristic musky odor which apparently warns the rest of the members of danger. The musk may also be used in assembling the dispersed members. On one occasion, a herd of seven peccaries were jumped from the brushy top of a hill; they fled in five directions. From the hill top, I watched the herd reassemble 30 minutes later about a quarter mile away. One adult, out of sight of the herd, was seen sniffing the air, bushes, and ground in returning to the herd on a route previously used by another member.

*Sense organs.*—In hat-, handkerchief-, and arm-waving experiments conducted in the field, it appears that peccaries have difficulty in seeing an object as large as a moving man over 100 yards away. Mule deer (*Odocoileus hemionus*) and peccaries have frequently been at the same waterhole when these object waving experiments were conducted. In all instances, the mule deer were able to detect the moving objects quicker than did the peccaries. In these same experiments, the mule deer showed more pronounced reactions to snapping of twigs and rubbing of rocks together than did the peccaries. In testing the olfactory ability of mule deer and peccaries, I sat at a waterhole on top of a large boulder and recorded the reactions of



both animals as they came in to drink. No pronounced differences between the mule deer's and peccaries' olfactory ability were observed. Thus, the mule deer appears to be superior to the peccary in sight and hearing ability, but no pronounced differences in the olfactory ability were observed.

*Reaction to rattlesnake.*—The peccary's reputation as a snake killer has been described many times (Seton, 1929; Hornaday, 1904; Cutright, 1940). In most instances, the actual accounts were second hand. Observations of antelope in the act of killing rattlesnakes have been made on two occasions (Williams, 1937). A captured rattlesnake (*Crotalus* sp.), approximately one and one-half feet in length, was tethered to an iron stake by a cement waterhole in the Tucson Mountains on October 22, 1956. The waterhole measured 4 x 5 feet in length and width. Three peccaries approached the waterhole at 7 p.m. (after dark) and proceeded to drink about a foot away from the tethered rattlesnake. The snake "buzzed", and the three peccaries withdrew rapidly from the area. Two of the peccaries came back to the waterhole ten minutes later, but this time they approached the waterhole on the side opposite the snake. The rattlesnake "buzzed" the entire time that the peccaries were drinking at the waterhole.

Fourteen mule deer approached the waterhole during this experiment which lasted for three hours. Their reactions were similar to those of the peccaries, except that deer were more nervous and cautious in approaching the tank a second time. Only two deer actually obtained a drink, and then they drank for only about thirty seconds each.

*Diseases.*—Little is known of the diseases of this species. Walker (1956) reported an adult female and a young peccary with the head region devoid of hair. The naked skin appeared rough in these two animals. They frequently came to the waterhole near the Arizona-Sonora Desert Museum during the dry seasons. An adult female shot by a hunter in southern Arizona during the 1956 hunting season had an infected left hind leg. The infection had spread over the entire leg and into the rear portion of the large intestine. The cause of this infection was undetermined. This animal was observed walking on three legs just before the hunter shot it. Another adult peccary taken by an archer in the Tucson Mountains had an abnormal canine tooth development (Neal and Kirkpatrick, 1957).

*Internal parasites.*—Internal parasites have seldom been reported from the collared peccary. Alicata (1932) reported a cestoda *Moniezia Benedeni* from a peccary. Schwartz and Alicata (1933) described two parasitic nematodes from the Texas peccary, and Jacobson (1941) reported the genus *Balantidium* from Arizona peccaries.

*External parasites.*—These parasites appear to be scarce on Arizona peccaries, but Jennings and Harris (1953) found that fleas were numerous and ticks common on fifty-two peccaries collected in Texas. Two adult animals, shot during the February, 1956 hunt in the Tumacacori Mountains of southern Arizona, were found to be heavily

infected with a large sucking louse. It was identified by Dr. Floyd G. Werner, Entomology Department, University of Arizona, as *Pecaroecus javellii* Babcock and Ewing, 1938. Seven peccaries in Arizona were found to harbor this species of louse. Babcock and Ewing (1938) described this organism as a new genus and species from a Texas peccary, and Eads (1951) reported this species again on peccaries collected in Texas. MaCalister (1869) and Ewing (1924) reported two different species of biting lice on the collared peccary.

Fleas were uncommon on Arizona peccaries, and only 3 of 85 wild peccaries were found to harbor these parasites. Four specimens of the human flea (*Pulex irritans* L.) and two specimens of the tropical hen flea (*Echidnophaga gallinacea*) were collected from the three peccaries. The fleas were identified by Dr. William L. Jellison of the Rocky Mountain Laboratory, Hamilton, Montana, and Dr. C. Andresen Hubbard, Tigard, Oregon. Jordan and Rothchild (1923), Eads (1951), and Jennings and Harris (1953) have reported a species of flea, *Pulex porcinus*, from the Texas peccary.

In 85 live-trapped and 5 hunter-killed peccaries examined in Arizona, only 2 were found to harbor ticks. A single specimen of each of *Dermacentor albipictus* (Packard) and *Ornithodoros turicata* (Duges) were collected from these two peccaries. The ticks were identified by Glen M. Kohls of the Rocky Mountain Laboratory. McIntosh (1932), Dunn (1933), Cooley (1938), and Eads (1951) have recorded eight different species of ticks from the collared peccary in Texas and Panama.

*Food habits.*—Knipe (1957) stated that cactus (*Opuntia* sp.) was the preferred food of most peccaries in Arizona. Jennings and Harris (1953) found that 107 stomach samples collected in South Texas contained 84 percent prickly pear, and 3 stomach samples collected in Trans-Pecos Texas contained 53 percent prickly pear and 39 percent lechuguilla (*Agave lechuguilla*).

In the present study, 36 stomach-content samples were collected, 32 during the February, 1956 hunt, 2 in November, 1955, 1 in December, 1955, and 1 in June, 1956. The samples were washed in tap water, when first collected, to remove the digestive juices and finely digested particles. After washing, the samples were spread out on newspapers to dry. The samples were stored dry and later separated.

Volumes of the various items were determined by water displacement in a graduate cylinder. Items under one cubic centimeter were recorded as a trace. Prickly pear (*Opuntia Engelmannii*) represented 84.5 percent of the total contents by volume, gramineae, 8.6 percent, unidentified debris, 5 percent, saguaro seeds (*Carnegiea gigantea*), 0.6 percent, and all others, 1.3 percent.

*Summary.*—Life history information on the collared peccary was obtained between September, 1955, and January, 1957, in southern Arizona. The main study area was located in the Tucson Mountains.

Breeding apparently occurs in all months of the year. Seventy-

four percent of the young were born during the summer months of June, July, and August. The average litter size is about 1.5. Females have four functional mammae and four rudimentary mammae.

Young peccaries weigh about one pound at birth. Thirty-one adult females averaged 45.7, and seventeen adult males averaged 43.8 pounds each.

Juvenile pelage was replaced by adult pelage before the age of four months in two captive young peccaries. Predators and disease appear to cause a heavy mortality in the young. Peccaries normally live in herds, but some males live alone. The scent gland is used in mating behavior and herd intercommunication. External parasites were uncommon on Arizona peccaries. The main food of the peccary in Arizona and Texas was prickly pear pads.

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## The Genus *Cambarus* in Louisiana (Decapoda, Astacidae)

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In 1950 the senior writer began publishing a series of four papers summarizing the biology of Louisiana crawfishes. Eighteen species in three genera (*Cambarellus*, *Orconectes*, and *Procambarus*) were included in the first three contributions (Penn, 1950, 1952, 1956). Field work and research subsequent to publication of the last two papers increased the number of known species and subspecies of the latter two genera in Louisiana. The present paper includes data on five additional forms in the fourth genus (*Cambarus*) and brings the known Louisiana crawfish fauna to twenty-nine species and subspecies.

### CAMBARUS Erichson, 1846

*Diagnosis*.—First pleopods of form I male terminating in two distinct parts: both short, usually heavy and bent caudad at about a 90° angle to the shaft of the appendage. Hooks present on the ischiopodites of the third, or third and fourth pereiopods of the male.

The genus is divided into several sections, of which only the *Diogenes* section is represented in Louisiana.

### DIOGENES SECTION

*Diagnosis*.—Cephalothorax ovate, compressed, without lateral spines. Rostrum without marginal spines. Chelae short and broad, depressed, ovate. Areola very narrow or obliterated in the middle. Eyes well developed. Hooks on ischiopodites of third, or third and fourth pereiopods of the male.

Four species are present in the state; one is represented by two subspecies.

### CAMBARUS DIOGENES DIIOGENES Girard

*Cambarus diogenes* Girard, 1852, Proc. Acad. Nat. Sci. Phila., 6:88; *Cambarus nebrascensis* Girard, 1852, Proc. Acad. Nat. Sci. Phila., 6:91; *Cambarus obesus* Hagen, 1870, Illus. Cat. Mus. Comp. Zool., 3:81; *Cambarus dubius* Osborn and Williamson, 1898, Ann. Rept. Ohio State Acad. Sci., 6:21 (*non dubius* Faxon); *Cambarus (Bartonius) diogenes* Girard, Ortmann, 1905, Proc. Amer. Philos. Soc., 44:120; *Cambarus diogenes diogenes* Girard, Hobbs, 1942, Univ. Fla. Publ., Biol. Sci. Ser., 3:164.

*Diagnosis*.—Ratio of cephalic portion of cephalothorax to areola always more than 1.40 (mean, 1.49); sides of cephalothorax ovate; cephalothorax length/width 2.49; areola obliterated; sides of rostrum non-parallel; antennal scale length/width less than 1.45; sides of antennal scale nearly straight and parallel. Annulus ventralis about 1.4 times as wide as long; fossa centrally placed; central sinus curving

dextrad posteriorly to the midline and then to posterior margin on midline.

*Type locality*.—"Near Washington, D. C."; type unknown, paratype in collection of the Academy of Natural Sciences in Philadelphia according to Faxon (1914); type of *C. obesus*, MCZ 195, from Lawn Ridge, Illinois.

*Color*.—Overall a drab subspecies. The ground color on the cephalothorax and abdomen dorsally shades from olive-green to brown; the ventral surface is cream colored. Chelae shade from olive-green at the base of the fingers to creamy-buff at the apices with both fingers red-tipped. Joints of pereopods reddish-brown. Young specimens are mostly olive-green, while older specimens are mostly dark brown. Hobbs and Marchand (1943) described two color variations in this subspecies at Reelfoot Lake, Tenn.; specimens seen alive from Louisiana are more nearly like their "solid colored phase."

*Specimens examined*.—From Louisiana we have seen 123 specimens from the following localities:

*Allen Parish*: 1.6 mi. W. Oakdale (TU 3383); *Bossier Parish*: 7 mi. W. Plain Dealing (TU 424), 4 mi. E. Ivan (MCZ, AMNH); *Caddo Parish*: *Shreveport* (HHH 10-1536-1); *Calcasieu Parish*: 3 mi. E. Holmwood (TU P-554); *Caldwell Parish*: 4 mi. E. Columbia (TU 430); *Cameron Parish*: Hackberry (HHH 3-2039-1); *Claiborne Parish*: 3 mi. E. Blackburn (TU 1450); *DeSoto Parish*: 0.5 mi. NE. Naborton (TU 3415), 4 mi. E. Mansfield (TU 3413), Frierson (USNM 23662, 23677, 28632; CM 74.962); *Iberia Parish*: 4 mi. SW. New Iberia (TU 1039); *Iberville Parish*: 8 mi. N. Indian Village (TU 950); *Livingston Parish*: 2.2 mi. S. Walker (TU 2819), Denham Springs (TU P-604), 2 mi. S. Weiss (TU 568); *Natchitoches Parish*: 5.9 mi. N. Chestnut (MCZ), 2 mi. S. Derry (TU 2914); *Ouachita Parish*: Wham (TU 2893), Monroe (TU P-422); *Pointe Coupee Parish*: Jacoby (TU 1007); *Sabine Parish*: Negreet (HHH); *St. Helena Parish*: 1.4 mi. W. Darlington (TU 3428), Liverpool (TU P-529), 5 mi. W. Chipola (TU P-541); *St. Tammany Parish*: 4 mi. N. Covington (TU 1989), Covington (TU 1503, 1985), Talisheek (TU P-824); *Tangipahoa Parish*: 1.4 mi. N. Kentwood (TU 3431), 2 mi. E. Wilmer (TU 3050, 3051), 3 mi. E. Amite (TU 220); *Union Parish*: 4.3 mi. S. Bernice (TU 3223); *Vernon Parish*: 11 mi. E. Leesville (TU 2926); *Washington Parish*: Sheridan (TU 182); *Webster Parish*: 3 mi. W. Springhill (MCZ, AMNH).

*Life History*.—Specimens have been collected in Louisiana from March through August, October, and November. Form I males have been found in March, April, and October; mature females from March through August. The smallest form I male from the state measured 32.0 mm in cephalothorax length. Ovigerous females have not been collected in Louisiana. The smallest juveniles (6 to 10 mm cephalothorax length) were collected from bodies of water in April and May, suggestive of a spawning season in March and April. This agrees with reports of ovigerous females of this subspecies from Florida and Indiana in April and May (Hobbs, 1942; Hay, 1891, 1918) and other more distant localities. The only record from another area at great variance is that of ovigerous females in Indiana in January by Bundy (1877).



The seasonal distribution of Louisiana collections is given in the following table.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Totals
♂♂ I			2	1						1			4
♂♂ II			3		1			6			1		11
♀♀			4	6	2	5	2	3					22
♂♂ juv				15	1	12							28
♀♀ juv			1	17	15	15	4	2					54
Totals			10	39	19	32	6	11		1	1		119

*Ecology.*—This crawfish is either a primary or secondary burrower. The adults remain in their burrows except at spawning time; the juveniles burrow along the edges of bodies of water and in seepage areas, hence they are frequently found in open water. A recent review (Williams and Leonard, 1952) of the burrowing habits, the burrows, and chimneys of this crawfish makes repetition here unnecessary.

On the other hand, relatively few carcinologists have recorded observations on the aquatic habitats of this subspecies, hence a brief review in addition to our notes seems appropriate. Creaser (1931) found adults in streams, rivers, and lakes only during the breeding season in Michigan; he made no mention of the habitats of the juveniles. Hobbs and Marchand (1943) found adults in streams in June and July in the vicinity of Reelfoot Lake, Tenn., and noted that "young specimens (one to two inches in length) were common occupants of streams, and in some of the very small streams. . . they seemed to comprise the entire crayfish population."

Of the 30 Louisiana lots with ecological data, only 5 are from burrows. The remainder were from aquatic habitats as follows: creeks (52%), ponds and upland sloughs (24%), overflow surface water (16%), and roadside ditches (8%). The majority (72%) were juveniles.

The physical and biological factors in the aquatic habitats were: shaded (54%), permanent (59%), clear colorless water (71%), flowing or static (50% each), shallow, *i.e.* less than 15 inches deep (74%), mud to sandy mud substrate (78%), without aquatic vegetation present (55%). The aquatic plants encountered, in order of frequency of occurrence, were *Vallisneria* sp., *Utricularia* sp., *Hydrocotyle* sp., and *Typha* sp.

#### CAMBARUS DIOGENES LUDOVICIANUS Faxon

*Cambarus diogenes* Girard (in part), 1852, Proc. Acad. Nat. Sci. Phila., 6:88; *Cambarus obesus* Hagen (in part), 1870, Illus. Cat. Mus. Comp. Zool., 3:81; *Cambarus diogenes* var. *ludoviciana* Faxon, 1884, Proc. Amer. Acad. Arts and Sci., 20:144; *Cambarus diogenes* Girard (in part), Shufeldt, 1896, The Observer, 7:85.

*Diagnosis.*—Ratio of cephalic portion of cephalothorax to areola always less than 1.30 (mean, 1.24); sides of cephalothorax more or

less parallel, or slightly ovate; cephalothorax length/width 2.24; areola obliterated; rostrum narrow; antennal scale length/width greater than 1.45; sides of antennal scale nearly straight and parallel. Annulus ventralis as long as wide with fossa on right side; sinus originating on right side, then turning medially to midline and from there continuing posteriorly on midline.

*Type locality*.—"New Orleans, La."; cotypes, USNM 5625 and MCZ 3617.

*Color*.—Ground color brilliant blue with ventral surface entirely cream. Abdomen with three longitudinal red stripes, base of telson and uropods marked with red as well as the margins of the uropods, but not the telson. Fingers of chelae red tipped. Colors are most brilliant on smaller specimens.

*Specimens examined*.—From Louisiana we have seen 183 specimens from the following localities.

*Assumption Parish*: Napoleonville (TU 2658); *Jefferson Parish*: Metairie (TU 3288, MCZ), Harahan (TU 2649), Waggaman (TU 2667), Bridgedale (TU P-643), Kenner (TU 2679); *Orleans Parish*: Audubon Park (AMNH, TU P-567, P-646, 3128), New Orleans (USNM 5504, 5625, 48820; MCZ 242; TU P-599); *St. Bernard Parish*: Breton Sound (TU P-600); *St. Charles Parish*: Luling (TU 3122), Bonnet Carré Spillway (TU 1823); *St. Tammany Parish*: Slidell (TU 2874); *Tangipahoa Parish*: 2 mi. N. Ponchatoula Beach (TU 2498); *Terrebonne Parish*: 0.8 mi. E. Dulac (TU 2882), Shriever (HHH), Houma (USNM 92415); *Washington Parish*: 5 mi. E. Varnado (HHH).

Previously this subspecies was recorded from New Orleans by Hagen (1870) as *C. obesus*, by Shufeldt (1896) as *C. diogenes*, and by Ellis (1919).

*Life history*.—Specimens of *C. d. ludovicianus* have been collected in Louisiana from January through May, July, August, and October through December. Form I males have been found in February, May, July, August and November; mature females from January through May, July and October through December. Ovigerous females are known from December and January, and the greatest numbers of small juveniles (6 to 10 mm cephalothorax length) have been taken in March. The smallest form I male and the smallest ovigerous female measured 32.8 and 35.0 mm cephalothorax length, respectively. The seasonal data for Louisiana collections are given in the following table.

	Jan.	Feb.	Mar	Apr	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Totals
♂♂ I			1		1		1	1			1		5
♂♂ II				3	2		3			1			9
♀♀			1	11	4	2	4			1	1		24
♀♀ (eggs)		2										1	3
♂♂ juv.				10	41								51
♀♀ juv.				13	64								77
Totals		2	2	37	111	3	8	1		2	2	1	169

*Ecology*.—This subspecies is apparently limited by ecological barriers to a relatively small area of Louisiana. It has been found only in the area described by Viosca (1933) as hardwood alluvial ridges and intervening swamps, marshes and lakes at or near Gulf level. This area is in the southeastern part of the state around the rim of Lake Pontchartrain and southward to within 50 miles of the Gulf. Only one collection, from the Pearl River valley in Washington Parish (TU 2964), has been made in a similar habitat above Gulf level. Only four of the 14 collections with ecological data were made from aquatic habitats, the other ten from burrows (7) or on the surface during heavy rains (3). The burrows excavated do not differ from those described for *C. d. diogenes* by various writers, nor do the chimneys differ from those described for this subspecies by Shufeldt (1896).

#### CAMBARUS HEDGPETHI Hobbs

*Cambarus argillicola* Faxon (in part), 1884, Proc. Amer. Acad. Arts and Sci., 20:116; *Cambarus fodiens* (Cottle) Creaser (in part), 1931, Pap. Mich. Acad. Sci., Arts and Ltrs., 13:269; *Cambarus fodiens* (Cottle) Penn, 1941, Abstr. Pap. N. O. Acad. Sci., 1941:8; *Cambarus hedgpethi* Hobbs, 1948, Proc. U. S. Nat. Mus., 98:224.

*Diagnosis*.—Rostrum without lateral spines; areola obliterated in middle; antennal scale length/width not over 2.50 (mean, 2.13); lateral margin of antennal scale straight, medial margin strongly curved. Chelae strongly depressed, with a prominent tuft of plumose setae along base of opposable margin of immovable finger; immovable finger with two prominent tubercles on opposable margin; males with hooks on ischiopodites of third pereopods only; mesial process of first pleopod of form I male so grooved as to appear slightly twisted.

*Type locality*.—"Lower middle part of the Aransas National Wildlife Refuge, Aransas County, Texas"; holotype, USNM 85146.

*Color*.—The following description is based on examination of living specimens collected in Livingston Parish in July. Overall this is a rather drably colored crawfish; all colors have a faded or "washed-out" appearance. Cephalothorax olive-tan dorsally, shading into a lighter hue of the same color laterally and ventrally. The dorsal surface may have a slight bluish cast in some lights. Abdomen of generally the same background color as the sides of the cephalothorax, with two faint, wide, bluish stripes running its full length and extending out onto the telson and uropods. Ventral edges of abdominal tergites light olive-tan. Pereopods generally of the same color as the sides of the cephalothorax; fingers of chelae tipped with orange-tinted pink.

*Specimens examined*.—We have seen 299 specimens from the following localities in Louisiana.

*Acadia Parish*: 2 mi. N. Church Point (TU 479); *Allen Parish*: Elizabeth (HHH, TU P-587); *Ascension Parish*: near St. Amant (TU P-551); *Bossier Parish*: Vanceville (TU 1412); *Calcasieu Parish*: Lake Charles (TU P-611); *Cameron Parish*: Ferrell (TU P-537); *Claiborne Parish*: 8 mi. E. Lisbon (TU 1456); *East Feliciana Parish*: 7 mi. E. Norwood (TU 2807); *Grant*

*Parish*: 1 mi. S. Magnolia Park (TU 1769); *Iberville Parish*: 1 mi. E. St. Gabriel (TU 828), Plaquemine (TU 1005), 8 mi. S. Indian Village (TU 1006), 10 mi. S. Bayou Sorrel (TU 1010), Gross Tete (TU 1016); *Jackson Parish*: 2.4 mi. W. Quitman (HHH); *Jefferson Parish*: Crown point (TU P-602), Kenner (TU 2679); *Lafayette Parish*: vicinity of Lafayette (TU 472, 2308, 2311); *Livingston Parish*: 1.1 mi. S. Walker (USNM, MCZ, TU 2818), Port Vincent (TU P-552); *Pointe Coupee Parish*: Torras (TU 1015); *Rapides Parish*: 3.6 mi. W. Lecompte (TU 2676); *St. Charles Parish*: vicinity of Paradis (HHH, MCZ, TU 3121); *St. Helena Parish*: 2 mi. S. Greensburg (TU 572); *St. James Parish*: 1 mi. E. Remy (TU 858); *St. Landry Parish*: 2 mi. S. Lawtell (TU 478); *St. Tammany Parish*: Talisheek (TU 3052); *Tangipahoa Parish*: 1 mi. W. Tickfaw (TU 217); *Union Parish*: 5.7 mi. SE Junction City (TU 3224), 7.9 mi. SW. Marion (TU 3226); *Washington Parish*: 6 mi. NW. Enon (TU 746); *West Feliciana Parish*: 8 mi. N. St. Francisville (USNM), Carney (TU 992).

Previously *C. hedgpethi* had been recorded from Orleans Parish as *C. argillicola* by Faxon (1885). This specimen (USNM 2262) was identified as *C. hedgpethi* by Hobbs (1948), who also added records from DeSoto Parish (USNM 23551, 23663). The only other published information on the species in the state was by Penn (1941, 1953) without specific locality or other data.

*Life history*.—In Louisiana collections have been made in all months except September and October. Form I males have been collected in February, June through August, November, and December; mature females only from November through April. Ovigerous and/or young-bearing females have been collected in November, December, February, and March. The smallest form I male and ovigerous female measured 21.0 and 20.5 mm cephalothorax length, respectively. The greatest numbers of small juveniles (*i.e.*, less than 10 mm cephalothorax length) have been collected in late spring and early summer: April through June. As the majority of our specimens are juveniles (266 of the 299) and as most of these were collected from aquatic habitats, and as all ovigerous or young-bearing females were taken from aquatic habitats, we assume that the females leave their burrows and seek open water before or shortly after oviposition. The only exception to this assumption is a lone ovigerous female taken from a burrow in Texas in February (Penn and Hobbs, 1958). Apparently the adults alone are primary burrowers, since outside the spawning season all adult specimens were taken from burrows. Seasonal data for Louisiana are given in the following table.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Totals
♂ ♂ I			1			1	2	1			2	2	9
♂ ♂ II						1		3				1	5
♀ ♀		2	5	1	2								10
♀ ♀ (eggs)			3	1							1	1	6
♀ ♀ (young)			3										3
♂ ♂ juv.			3	1	55	2	32	11	7			5	116
♀ ♀ juv.			2	4	66	10	49	11	6			2	150
Totals	2	17	7	123	12	83	24	17			3	11	299

*Ecology.*—The 40 Louisiana collections have come from a variety of habitats, as summarized briefly in the table below.

Habitat	Percent of Total Collections
Temporary situations: .....	62.5
Ditches (mostly roadside) .....	27.5
Burrows .....	25.0
Surface water (overflow puddles) .....	10.0
Permanent situations: .....	37.5
Sloughs, swamps, and swamp pools .....	15.0
Ponds .....	15.0
Creeks .....	7.5

The various physical and biological factors in all aquatic habitats combined (*i.e.*, excluding burrows) may be summarized in the statement that *C. hedgpethi* occurs more frequently in shallow water, *i.e.*, less than 15 inches deep (81%), that is either clear or turbid (50% each), temporary or permanent (50% each), static (82%), and exposed to full sunlight (64%). Most collections were from habitats with mud substrate (85%) and with sparse aquatic vegetation present (62%). The aquatic plants recorded, in order of frequency and abundance, were *Jussiaea* sp., *Polygonum* sp., *Iris* sp., and *Hydrocotyl* sp.

The burrows recorded were all in localities where the soil had a clayey consistency. Each burrow had only one opening and most had small, neatly constructed chimneys; the tallest chimneys recorded were about six inches high. Each burrow was without branches and terminated at soil-water level in a larger pocket or chamber; the depth of burrows ranged from 8 to 40 inches.

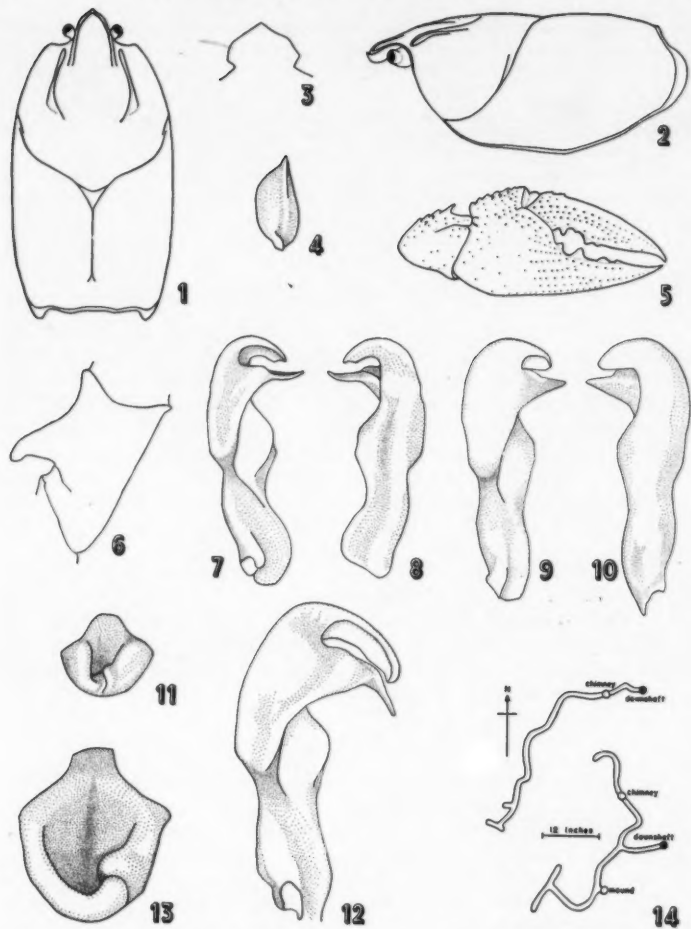
#### *Cambarus oryktes*, sp. nov.

*Diagnosis.*—A member of the *Diogenes* section of the genus (*i.e.*, with areola obliterated and longer than half of the cephalic section of the cephalothorax, chelae short and broad). Rostrum without lateral spines; antennal scale not extending beyond tip of the rostrum; eyes reduced, but pigmented; hooks on ischiopodites of third pereopods; mesial process of first pleopod of form I male grooved so as to appear twisted; chela with base of immovable finger bearded and base of dactyl excised.

*Holotype male, form I.*—Body ovate; abdomen narrower than cephalothorax (8.0-11.00 mm in widest parts respectively). Greatest width of cephalothorax (Figs. 1, 2) greater than greatest depth (11.5-10.0 mm). Greatest width of cephalothorax slightly caudad of caudodorsal margin of cervical groove.

Areola obliterated in middle; cephalic section of cephalothorax 1.3 times as long as areola; length of areola about 43 percent of entire length of cephalothorax.

Rostrum directed cephaloventrad with acumen curved cephalad;



FIGS. 1-14.—*Cambarus oryktes*, sp. nov.: 1 and 2—Dorsal and lateral views of cephalothorax of form I male; 3.—Epistome of form I male; 4.—Antennal scale of form I male; 5.—Chela and carpus of form I male; 6.—Hook on ischiopodite of form I male; 7 and 8.—Mesial and lateral views of first pleopod of form I male; 9 and 10.—Mesial and lateral views of first pleopod of form II male; 11.—Annulus ventralis of mature female. *Cambarus byersi* Hobbs: 12.—Mesial view of first pleopod of form I male; 13.—Annulus ventralis of mature female. *Cambarus oryktes*, sp. nov.: 14.—Diagrams of horizontal tunnels. (Pubescence removed from all structures illustrated in Figs. 1-13.) All drawings were made by Miss Sue Blackshear from pencil sketches by the senior author.



upper surface shallowly excavate; margins converge slightly from base and turn abruptly mesiad apically at the base of the short acumen; no lateral spines, hence acumen is not distinctly set off from the rest of the rostrum. Rostrum with a few punctations on basal half; apical half glabrous. Rostral margins weakly inflated. Postorbital ridges low, terminating anteriorly without spines; shallowly excavate laterally. Branchiostegal spines absent.

Surface of cephalothorax non-granulate, but with a moderate number of punctations.

Cephalic section of telson with two spines in each caudolateral corner.

Epistome (Fig. 3) wider than long, terminating anteriorly without a definite spine.

Eyes reduced, but pigmented and apparently normal.

Antennules of usual form. Antennae broken (but not extending beyond caudal margin of the cephalothorax in any of the other specimens examined). Antennal scale (Fig. 4) reaching tip of rostrum; total length approximately one-fourth that of the areola (2.5-10.0 mm); widest point near middle; lateral margin curved and terminating anteriorly in a weak spine.

Right chela (Fig. 5) depressed, palm inflated; thickness of palm about 55 percent of its width. Fingers gently curved ventrally from their bases, gaping for their entire length; fingers punctate above and below; palm moderately punctate above. Palm with six tubercles along its mesial margin. Immobile finger with four tubercles on opposable margin; second tubercle from base of finger largest. Dactyl (movable finger) with six tubercles on opposable margin; third tubercle from base largest. Basal half of immobile finger conspicuously bearded.

Carpus (Fig. 5) longer than wide, slightly longer than mesial margin of palm (6.5-5.2 mm); with a prominent longitudinal furrow above. Mesial margin with seven tubercles irregularly arranged, the largest one at the distal end. Under surface with one small tubercle.

Hooks (Fig. 6) present on ischiopodites of third pereopods. Hooks simple; length of hook about one-half the greatest width of the ischiopodite.

Coxopodite of fourth pereopod with a prominent, subspherical ventrocaudal projection.

First pleopod (Figs. 7, 8) reaching to middle of the coxopodite of the third pereopod when abdomen is flexed; terminating in two distinct parts. Central projection corneous and bladelike, recurved caudad at slightly greater than a right angle to the main shaft of the pleopod; fusion line of its two components clearly marked. Mesial process grooved so as to appear twisted; not bulbous; recurved caudolaterad at slightly more than a right angle to the main shaft of the appendage.

*Morphotype male, form II.*—Similar to holotype in general appearance and bodily proportions; chelae and hooks on ischiopodites

of third pereopods reduced. First pair of pleopods (Figs. 9, 10) reaching to middle of coxopodites of third pereopods when abdomen is flexed; all terminal elements reduced, blunted and non-corneous.

*Allotype female*.—Similar to holotype in general appearance and bodily proportions; chelae reduced; ventrocaudal projection of coxopodite of fourth pereopod not present. Annulus ventralis (Fig. 11) immovable, slightly wider than long; median surface somewhat flattened and cephalic margin fused with and indistinguishable from sternum of fifth thoracic segment; lateral and caudal margins precipitously raised from median area; the sinus originates near the midline on the cephalic face of the caudal margin, then forms a slight sinistral arc to the caudal face where it terminates.

*Measurements*.—Data from the types are given in the following table in millimeters.

	Holotype	Allotype	Morphotype
Cephalothorax			
Total length	23.5	22.5	25.0
Width (greatest)	11.5	10.5	11.5
Depth (greatest)	10.0	9.6	10.0
Areola length	10.0	9.4	10.5
Rostrum			
Length	3.5	4.0	4.0
Width	3.0	2.8	3.8
Antennal scale			
Length	2.5	2.2	2.5
Width (greatest)	1.0	0.9	1.0
Epistome			
Length	1.1	1.1	0.9
Width	1.4	1.2	1.2
Abdomen length (including telson)	21.5	21.5	22.0
Chela			
Length of outer margin	17.3	15.0	18.3
Length of dactyl	12.8	10.0	12.3
Width of palm	9.0	7.0	8.3
Thickness of palm (greatest)	5.0	4.3	5.0

*Color*.—In adult living specimens of both sexes from the Covington area the dorsal surface of the cephalothorax is a homogeneous blackish-brown. This color extends onto the abdomen as a mid-dorsal stripe that narrows posteriorly and terminates at the base of the telson. Lateral to the mid-dorsal stripe the abdomen has a reticulate color pattern of blackish-brown on tan. Ventrolaterally the cephalothorax is tan. The fingers of the chela are bluish-black with dark tan tips and the palm has the reticulate pattern and same colors as the lateral surfaces of the abdomen. The carpus resembles the fingers in color.

In some living specimens and all recently preserved individuals the homogeneous areas of the cephalothorax and chelae have a slightly purplish cast. This latter is suggestive of the color descriptions by Hobbs (1941) for *C. byersi*.

*Type locality.*—The holotype was taken from shallow water in a roadside ditch at Alton, St. Tammany Parish, La. No other crawfishes were present. The allotype and morphotype were dug from burrows in the bottom of a dry roadside ditch between 6.5 and 10 miles northeast of Covington, St. Tammany Parish, La. No other crawfishes were collected although larger burrows (unexplored) presumably were made by specimens of *C. diogenes diogenes*.

*Disposition of types.*—The holotype, allotype and morphotype are deposited in the United States National Museum, Numbers 101,735, 101,736, and 101,737, respectively. Of the 32 paratypes, 1 ♂ I, 1 ♂ II, and 1 ♀ are in the personal collection of Dr. Horton H. Hobbs, Jr., at the University of Virginia, and the remaining specimens (1 ♂ I, 6 ♂ ♂ II, 5 ♀♀, 1 ♂ juv, 15 ♀♀ juv) are in the Tulane University invertebrate collection.

*Geographic distribution.*—The type series was collected from two localities in St. Tammany Parish, La. These records are (1) Alton, 24 Dec. 1952, W. G. Moore, holotype ♂ I; (2) 6.5 to 10 miles NE. Covington: 17 April 1954, H. H. Hobbs *et. al.*, morphotype ♂ II and 1 ♂ II (HHH 4-1754-50); 1 April 1958, G. Marlow, 1 ♂ I, 3 ♂ ♂ II, 1 ♀ (TU 3550); 4 April 1958, G. H. and M. H. Penn, 1 ♂ I, 2 ♂ ♂ II, allotype ♀, 3 ♀♀, 7 ♀♀ juv (TU 3551); 11 April 1958, G. H. Penn and G. Marlow, 1 ♂ II, 2 ♀♀, 1 ♂ juv, 8 ♀♀ juv (TU 3555).

*Variation.*—No noteworthy variations in shapes of structures or bodily proportions were observed in the specimens examined.

*Relationships.*—*Cambarus oryktes* obviously is a species of the *Diogenes* section, and within the section clearly is most closely related to *C. byersi* Hobbs (1941:118). Males of *C. oryktes* may be distinguished readily by the straighter first pleopod with proportionately shorter terminal elements (cf. Figs. 7 and 12); females may be distinguished by the sculpturing of the annulus ventralis (cf. Figs. 11 and 13); and, all mature specimens may be distinguished by the bearded immovable finger.

*Ecology and life cycle.*—This crawfish is probably a primary burrower according to the definitions of Hobbs (1942). All specimens except the holotype were taken from burrows in a roadside ditch. The burrows that we excavated were all complex and marked at the surface by either well-constructed five to six-inch high chimneys, or small mounds of excavated mud. The horizontal tunnels (Fig. 14) were just below the level of weed roots (five to six inches) in the ditch bottom. The main down-shaft extended from about 18 inches to over three feet in an almost vertical direction. The two areas from which these crawfishes were collected are characterized as longleaf pine flats (Viosca, 1933) in the Pearl River drainage in which the soil is a mixture of sand and yellow clay.

Judging from the size of the juveniles (5 to 7 mm cephalothorax length) in early April in the burrows of mature females we postulate

that egg-laying occurs in February and March. Form I males were collected in late December and April.

*Derivation of name.*—The species name is derived from the Greek word *oryktes*, meaning "digger," in reference to the burrowing habits of the animals.

CAMBARUS DISSITUS Penn

*Cambarus dissitus* Penn, 1955, Tulane Stud. Zool., 3:73.

*Diagnosis.*—Rostrum without lateral spines; antennal scale not extending beyond tip of rostrum; areola obliterated or very narrow in middle; chelae depressed apically, palm inflated; hooks on ischiopodites of third and fourth pereopods; mesial process of first pleopod of form I male so grooved as to appear twisted; central projections of the first pair of pleopods recurved caudio-mesial so that *in situ* they overlap in the mid-ventral line.

*Type locality.*—"Three miles east of Choudrant, Lincoln Parish, Louisiana"; holotype, USNM 98125.

*Specimens examined.*—Thirty-four specimens are known; all of these were included in the type series from Caldwell and Lincoln parishes.

*Life history and ecological observations.*—Form I males were taken in February, May, and December, mature females only in February and May. All were dug from shallow burrows in the upland shortleaf and longleaf pine hills of Caldwell and Lincoln parishes.

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## Distribution of Tetraploid and Diploid *Tradescantia ohiensis* in Michigan and Adjoining Areas

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*Tradescantia ohiensis* exists in a wild state in a diploid form and a tetraploid form which cannot be distinguished by morphological criteria. This paper reports the detailed distribution of diploid and tetraploid *T. ohiensis*. Since the area studied includes the northern limit of the range of the species and is far from its center of distribution, it seems a significant area in which to study the role of polyploidy in distribution.

Edgar Anderson has made extensive studies of the distribution of diploid and tetraploid *Tradescantia ohiensis* (summarized in Anderson, 1954). He found tetraploids to predominate throughout most of the United States east of the Great Plains. He found diploids most abundant in Texas where diploids of other species of *Tradescantia* are centered, but he also found diploids in isolated areas of Indiana, Iowa, Kentucky, Michigan, and Louisiana.

Except for diploid plants near the outer edges of the range of the species, the pattern of distribution plotted by Anderson in *T. ohiensis* (and in other species with both diploid and tetraploid races) suggested that the more aggressive tetraploids spread great distances from the place where the original doubling occurred, while the less adaptable diploids remained near the center of distribution of the species. The presence of diploids near the periphery of the range, however, is not explained by the above assumption alone.

The area (outlined with stippling, Fig. 1) studied intensively by the author includes lower Michigan and enough of Indiana and Ohio to furnish a unit of investigation. On the basis of a study of herbarium records, and after intensive efforts to find the species growing farther north, the author is convinced that the northern limit of the distribution of the species is essentially as shown in Figure 1.

Determinations of chromosome number were made from acetocarmine squashes of dividing microspores and microspore mother cells. Occasionally determinations were made from examination of hydrolyzed root and leaf meristems. Much of the determination was done in the field where the plants were collected, though many chromosome numbers were ascertained from plants taken to the laboratory.

<sup>1</sup> This paper is part of a Ph.D. dissertation directed by Dr. Robert L. Lowry and submitted to the Graduate School of the University of Michigan in 1953. The author is grateful to Dr. Lowry, Professor H. H. Bartlett, Dr. W. C. Steere, Dr. Edgar Anderson and many others for their assistance.



It became apparent during the course of the investigation that diploids and tetraploids rarely overlapped in their distribution. Tetraploids were far more numerous than diploids, but diploids were found in several extensive areas. In many of these areas, the diploids formed considerable populations. Diploids were by no means rare in the area studied. The chromosome number of a plant could almost be predicted from a knowledge of where the plant was collected. There was some overlapping in Washtenaw County, Michigan, particularly at Dexter where diploids and tetraploids were growing in a mixed stand. Plants at this station were studied intensively. Although some plants had irregular chromosome numbers, no triploids were found.

Diploids were found (1) in the region about Berrien County, Michigan, (2) in an area extending across northern Indiana, (3) in an area centered at the northwest corner of Washtenaw County, Michigan, and (4) in the counties along the southwest shore of Lake Erie. Diploids were also found on Squirrel Island in the Detroit River. A diploid station in White County, Indiana, is indicated on Figure 1 because of a plant transplanted from there to the Botanical Gardens of the University of Michigan. Although diploids were found in various parts of Ohio, the author has never found a tetraploid *T. ohiensis* growing in that state.

Tetraploids were distributed in a continuous pattern, unlike the diploids which were found in widely separated areas. Most tetraploids in Michigan were found in the area delimited by the Valparaiso,

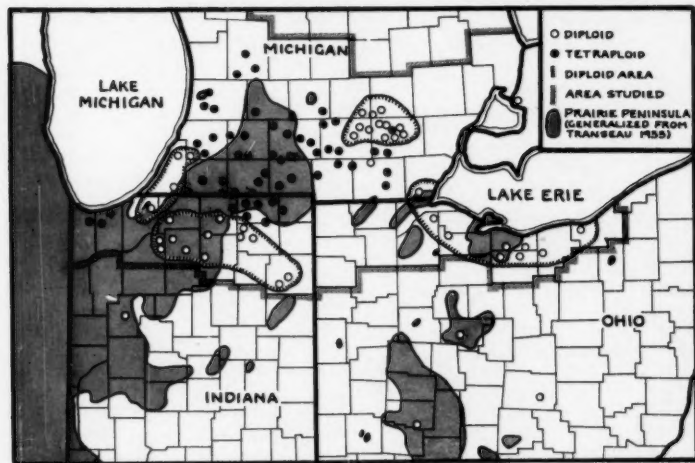


Fig. 1.—Collecting stations for diploid and tetraploid *T. ohiensis* in, and adjacent to, the area of investigation.

Charlotte, and Mississinawa Moraines. Tetraploids beyond that area extended from the main group along outwash channels.

*Tradescantia ohiensis* grows best in light soils and in habitats where it receives abundant light. The species seems to be excluded from regions of heavy soil (Fig. 2). This may be due to the direct influence of the soil, or to the vegetation which covers this soil. Neither diploids nor tetraploids were found growing extensively in areas originally covered by beech-maple forest. The species thrives best where prairies originally existed according to interpretations made from the original surveyors' data (Chapman, 1944; Gordon, 1936; Hartesveldt, 1951; Kenoyer, 1930, 1934, 1940; Merk, 1951).

The pattern of distribution of tetraploids in the area studied conforms in general to the pattern of Transeau's (1935) Prairie Peninsula (Fig. 1). The coincidence is much closer in general pattern than it is in extent. In addition, tetraploids in the heart of the Prairie Peninsula occur in greater numbers than in the surrounding region.

Although *T. ohiensis* is weedy by nature and able to grow under a variety of conditions, tetraploids were found growing under a greater range of conditions than the diploids. Tetraploids were more common than diploids in disturbed areas, and were also found in the driest, best-drained areas. An extreme example is the collection from Allegan State Park, Michigan, where tetraploids grew in hot, dry sand along with *Opuntia*.

The distribution of tetraploids and diploids was correlated with that of the soils in which they were growing (Table I). Soils were

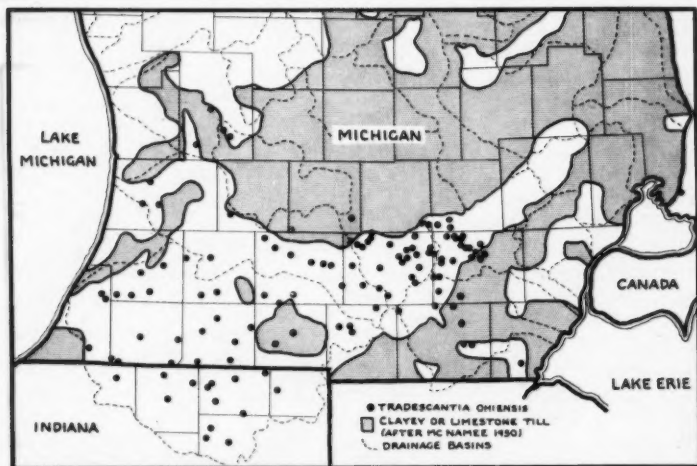


Fig. 2.—The distribution of *T. ohiensis* in relation to soils and drainage basins.

TABLE I.—Percentage of diploids and tetraploids in various soil types

	Tetraploid	Diploid
Sandy loam	60.4%	47.0%
Loam	15.1	8.8
Sand	13.2	0.
Loamy sand	7.5	11.7
Peat and muck	3.8	32.4

classified with the help of county soil maps and confirmed by field observations. Almost one-third of the diploids were found in regions of peat or muck; tetraploids were seldom found growing in such places. A characteristic site for diploid *T. ohioensis* is at the edge of a wet meadow, spreading from there to nearby roadsides and ditches.

#### DISCUSSION

The patterns of distribution in the area studied, particularly the disjunct distribution of the diploids, suggest that the diploids are relics of a time when these plants were more widely distributed. It seems probable that diploids spread from the south after the retreat of the glaciers and before the establishment of beech-maple forests and other climax vegetation which would exclude diploid *T. ohioensis*. When climatic and successional changes brought many of these areas into dense forest, the diploids were reduced to relict populations in favorable situations. With the advent of man, bottomlands were drained and forests were felled. The diploids were destroyed in some areas favorable for agriculture. The plants found acceptable niches in artificially treeless areas such as railroad embankments and roadsides.

A favorable time for the expansion of the range of tetraploid *T. ohioensis* into the area studied would have been the Xerothermic Period, when the prairies and bur oak forests were spreading north and east in the Prairie Peninsula (Sears, 1942). With the subsequent cooling of the climate and the closing of the forests, *T. ohioensis* would have been restricted to prairie openings, edges of prairie relics, and similar open habitats. According to Sears (1948), there were cycles of increasing and decreasing warmth within the broader cycles of post-glacial climatic change. The oscillations of the prairie-forest border would have favored tetraploid *T. ohioensis* which does well in regions of unstable vegetation.

When man cut the forests, "artificial prairies" in the form of mowed roadsides and railroad embankments made a network across the whole area. Populations isolated by the development of forests would have been brought together again in agrarian times, establishing the continuous distribution of the tetraploids. Present day conditions apparently favor the further spread of tetraploid *T. ohioensis*.

According to Hagerup (1932) and others who have ascribed in-

creased tolerance of adversity to tetraploids, one might expect to find diploids excluded from the coldest parts of the range of the species. When the collecting stations in Michigan were plotted on a map showing mean annual temperatures, the above correlation was shown not to be the case.

In assessing the role of polyploidy in the differential distribution of diploid and tetraploid *T. ohiensis*, the author attributes great importance to polyploidy as a basis for reproductive isolation of a part of the population. It may have been that the tetraploids arose from a part of the diploid population better adapted to dry conditions than most of the diploids. The original genes, and those modified later by mutation within the two populations, would be selected independently according to the prevailing environmental forces to which each population was subjected. Once differences in the basis for selection and in distribution arose, these differences would be further reinforced by the circumstance of growing in a particular place when major changes in climate or vegetation occurred.

Another important factor influencing the differential distribution of diploids and tetraploids is the ability of tetraploids to do well under a wide range of circumstances and under unstable conditions. One characteristic of polyploids which would equip them to adapt to varied conditions is the subtler range of variation which they exhibit due to the nature of their segregation. Anderson and Diehl (1932) pointed out why this might be expected; they used their observations of flower colors of *Tradescantia* as an illustration. The author's observations of color differences in diploids and tetraploids confirmed their finding that diploids are more likely to have sharply defined colors, while tetraploid populations are more likely to display a finely graded range of intermediate colors. It seems reasonable to expect that a similar situation would exist in regard to various adaptive characteristics and that because of this, tetraploids might be better able to survive in varied habitats.

Since the tetraploids have four genomes instead of two, many recessive genes and gene combinations are not regularly exposed and thus subjected to strong selection. For this reason, the tetraploids would be expected to have a wider complement of unselected genes. When genes ordinarily unexpressed are expressed through irregularities in meiosis, or other sources of recombination, new modifications of the plant would arise. Some of these modifications might fit the plant for survival, and under unstable conditions the ability to produce new variations would be of considerable advantage to the tetraploid.

#### SUMMARY

The distribution of diploid and tetraploid *Tradescantia ohiensis* in Michigan and adjoining areas is reported. Tetraploids were found to be more abundant in the area, and to grow in drier and more disturbed habitats than diploids. Considerable populations of diploids

were found, but they were noted to have a disjunct distribution. The author proposes that diploids formerly were widespread in the area and that they have been restricted to relict populations by changes in climate, drainage, and vegetation. It is suggested that tetraploids entered the area later, presumably during the time of the advance of prairie vegetation. Differences in distribution of diploids and tetraploids are attributed to reproductive isolation, historical circumstances, and the greater adaptability of tetraploids due to their greater complement of unselected genes.

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## Distribution, Habitat, and Abundance of the Topeka Shiner *Notropis topeka* (Gilbert) in Kansas

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### DISTRIBUTION

*Notropis topeka* (Gilbert) occurs from "Minnesota and South Dakota south through Iowa, Nebraska, Kansas, and Missouri" (Moore, 1957:134). Compared with distributions of other plains fishes, this range is small. No other fish has a similar area of distribution.

In Kansas, *N. topeka* has been reported from scattered localities that indicate its presence throughout the northern part of the state (Kansas River Basin) and in part of the Arkansas River Basin in south-central Kansas (Fig. 1). Approximately 37 localities are represented, 10 of which are west of 97° longitude. Nine of the 10 western records were obtained between 1882 and 1887 when the first general surveys of fishes were made in Kansas (Gilbert, 1885:98, 1886:210, 1889:39; Cragin, 1885:108; Evermann and Fordice, 1886:185; Hay, 1888:245, 248, 251, 252 [as *Notropis aeneolus* Hay], 246). The tenth record is a single specimen (KU 3108) obtained by A. B. Leonard and A. B. Williams from Cherry Creek, Cheyenne County, in April, 1947. Other recent collections west of 97° longitude have not included Topeka shiners. Breukelman (1940a) failed to find them in extensive surveys of streams in northwestern Kansas, and in 1958, Cross and B. C. Nelson did not find *N. topeka* at any of 30 western localities, including all those cited by Gilbert, Cragin, and Hay.

In the Kansas River Basin east of 97° longitude, *N. topeka* was reported from three localities between 1882 and 1887 (Gilbert, 1884 [types from Shunganunga Creek, Shawnee County, described as *Cliola (Hybopsis) topeka*], 1886:210; Graham, 1885:73). Graham's record may be erroneous, because it evidently was based on the same collection from the Missouri River that was reported by Jordan and Meek (1886:12-14), who did not list the Topeka shiner from that locality. Breukelman (1940b:380), reporting on fish in the University of Kansas Museum of Natural History, tabulated 27 specimens from the "Kansas [river], and tributaries not otherwise named." Presumably, this record refers to specimens collected by the State Biological Survey in 1912, from Rock Creek, Douglas County. Jennings (1942:365) listed *N. topeka* from two localities, one of which is the only record from the Marais des Cygnes System (Missouri River Drainage). Minckley (1956:353-354) reported one additional locality in the Kansas Basin. The species is now known from many other streams in the eastern part of the basin, mostly in the Flint Hills Region.

All of the older records from the Arkansas River System are west of 97° longitude, except for two specimens (formerly Indiana Uni-



versity 4605, now at the University of Michigan Museum of Zoology) that are labeled "Winfield, Kansas" (Cowley County). Breukelman (1940b:380) listed specimens in the University of Kansas collections from "Neosho [river], including Spring River"; however, we are unable to locate these specimens, or data upon them, and have not plotted the record in Figure 1. In intensive recent collecting in the Arkansas System, *N. topeka* has been found only in the Cottonwood River Drainage (Cross, 1954:310, and unpublished records obtained by Breukelman).

#### HABITAT

Evermann and Cox (1896:403) described the habitat of *N. topeka* as follows: "All the waters in which we took it were pond-like, isolated portions of streams which dry up in parts of their course during dry weather. These ponds are partly supplied from small springs, the water is usually rather clear and cool, and there is an abundance of water vegetation. The bottom is mostly soft mud." Churchill and Over (1933:53) indicated that in South Dakota the Topeka shiner is found only in "small creeks of the eastern and southern parts of the state."

In Boone County, Iowa, Starrett (1950:126-127) found Topeka shiners most often in vegetated pools of small streams with sand-silt bottoms. Also in Iowa, Harlan and Speaker (1956:98) considered the species to be "essentially a fish of wide expanses of sandy shoals."

In our studies in Kansas, the Topeka shiner has been found almost exclusively in quiet, open pools of small, clear streams that drain up-

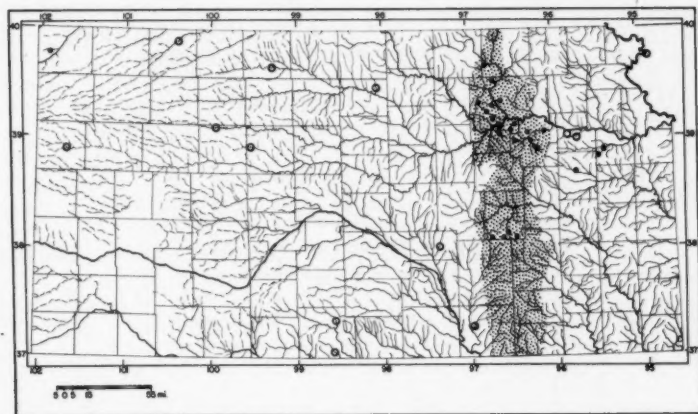


Fig. 1.—Distributional records of *Notropis topeka* in Kansas. Circles = records obtained in 1882-1889; dots = records obtained subsequently, mostly in recent years. The shaded part represents the Flint Hills Area.

land prairies. These streams are characteristically a series of large pools (up to 100 feet in length and more than 2 feet in depth) connected by short riffles and smaller pools; their flow is usually less than five cubic feet per second. Stream bottoms are predominantly gravel, with some rubble and sand. The bottoms of the largest pools sometimes consist of bedrock or clay hardpan, overlain by a thin layer of silt. In summer, the pools often develop plankton blooms, but rooted aquatic vegetation is uncommon. The Topeka shiner is most common in pools of this kind, and is pelagic in habit.

*N. topeka* occupies riffles only when the species is exceptionally abundant. It is rarely found in streams that maintain a continuously strong flow, and is not found in streams that are muddy and highly intermittent. Many of the streams where Topeka shiners occur approach intermittency in summer; however, pools are maintained at fairly stable levels by percolation through the gravel or by springs.

#### ASSOCIATED SPECIES

Several associates of *N. topeka* are generally abundant in Kansas streams, despite wide variations in habitat: red shiner, *Notropis lutrensis* (Baird and Girard); sand shiner, *N. stramineus* (Cope); fathead minnow, *Pimephales promelas* Rafinesque; black bullhead, *Ictalurus melas* (Rafinesque); green sunfish, *Lepomis cyanellus* (Rafinesque); and orangespotted sunfish, *L. humilis* (Girard). Other species that almost always occur with *N. topeka* have more restricted distributions, being found most often in clear, spring-fed streams.

In the Kansas River Basin, fishes that have most often occurred with *N. topeka* in our collections are: white sucker, *Catostomus commersoni* (Lacépède); creek chub, *Semotilus atromaculatus* (Mitchill); southern redbelly dace, *Chrosomus erythrogaster* (Rafinesque); common shiner, *N. cornutus* (Mitchill); bluntnose minnow, *P. notatus* (Rafinesque); stoneroller, *Camptostoma anomalum* (Rafinesque); orangethroat darter, *Etheostoma spectabile* (Agassiz); and johnny darter, *E. nigrum* Rafinesque. Another close associate is the crayfish, *Orconectes neglectus* (Faxon), which has a restricted distribution in the Kansas River Basin, approximating that of the Topeka shiner. Formerly, *O. neglectus* was more widespread than at present (Williams and Leonard, 1952:987).

In the Arkansas River Basin, fishes found with the Topeka shiner include the rosyface shiner, *N. rubellus* (Agassiz); redfin shiner, *N. umbratilis* (Girard); striped shiner, *N. zonatus* (Agassiz); bluntnose minnow; stoneroller; fantail darter, *E. flabellare* Rafinesque; and orangethroat darter.

#### ABUNDANCE

Nearly all reports upon *N. topeka* indicate scarcity, either by direct statement or by inference from the number of specimens taken. In South Dakota, Churchill and Over (1933:53) stated that the species

was found only "occasionally," and that it was not "sufficiently numerous to be of particular importance" as a bait or forage fish. Harrison (1949:337), Starrett (1950:117, 121), Cleary (1953:632), and Harlan and Speaker (1956:98), all implied that the species is rare in Iowa, the last authors stating that collections there often consist of only one or two specimens. Most records from Kansas are based on relatively few specimens, which comprised a very minor part of the total number of fish from the localities studied.

Several changes in abundance, locally and geographically, are evident from recent collections and from historical records in Kansas. These changes seem to correlate with short-term fluctuations in water-levels during wet and dry periods, and probably with long-term changes in climate and land-use that have influenced stream-habitats throughout the state.

Rainfall in Kansas was comparatively great from 1940 through 1951, culminating in record floods in 1951; this cycle was followed by five years of drought. Garrett (1956:3) reported that the three years, 1952-1954, were the driest such period in the history of the state, with five inches less precipitation than was recorded in the driest previous three-year period (1932-1934). The drought continued with increasing intensity until 1956; consequently, streams of Kansas probably became lower in 1956 than at any previous time.

Deep Creek, Riley County, in the Flint Hills Area, normally flows continuously, but was intermittent along most of its course in 1956. Deep Creek is a small stream with high gradient, draining approximately 70 percent grassland and 30 percent cultivated fields (Minckley, 1956:351). Cultivated areas are primarily in the narrow stream valley; virgin bluestem prairie occurs along tributaries and on the adjacent uplands.

Topeka shiners comprised seven percent of the fish collected from Deep Creek by Minckley (1956:353) in the spring of 1956. In the fall of 1956, *N. topeka* comprised approximately 20 percent of fish collected from this stream. The Topeka shiner had spawned successfully, but reproduction by other species was poor during intermittency in 1956. In 1957, normal flow was restored following slightly above-normal rainfall in May and June. Collections in August and December, 1957, and March, 1958, indicated lack of spawning success by *N. topeka* and successful spawning by other species in 1957 (Fig. 2). Examination of the scales of a random sample of 66 Topeka shiners collected on October 13, 1956, revealed that 50 belonged to the 1956 year class (20-43 mm total length, average 28 mm), 13 to the 1955 year class (43-56 mm, average 48 mm), and three to the 1954 year class (51-64 mm, average 58 mm). No Topeka shiners of the 1957 year class were taken in 1957 or 1958; specimens collected in March, 1958, ranged from 48 to 61 mm total length (average 55 mm), and most belonged to the 1956 year class.

A nearby stream, Mill Creek in Wabaunsee County, is physically similar to Deep Creek except that it normally has greater flow. In

1953, Mr. James Booth of the State Biological Survey, made 30 collections at 21 stations throughout the Mill Creek Drainage. He obtained only two specimens of *N. topeka*, both young-of-the-year, and both from small tributaries of the mainstream. At the time of Booth's survey, Mill Creek and most of its tributaries were flowing. In 1955 and 1956 Mill Creek became intermittent. In 1956-1957, the Topeka shiner was common in several collections that we made at stations previously worked by Booth. Two of our collections, obtained by brief seining, included more than 100 specimens. Nearly all belonged to the 1955 or 1956 year class, with the latter predominating.

Indications of increased populations from spring 1956 to summer 1957 were found in two other Flint Hills streams, Mill Creek (Riley County) and Carnahan Creek (Pottawatomie County). In the course of surveys of these streams in 1956, a class in fisheries management at Kansas State College, Manhattan, obtained one specimen of *N. topeka* from Carnahan Creek and none from Mill Creek. In 1957, we collected Topeka shiners at three of five stations on Carnahan Creek, and at our single station on Mill Creek.

Conversely, reductions in abundance seem to have occurred in Shunganunga Creek (Shawnee County), Wildcat Creek (Riley County), and Rock Creek (Douglas County). Series of *N. topeka* were collected from Shunganunga Creek in 1882-1884 (Gilbert, 1884:13, 1885:98; Cragin, 1885:108). Our collections since 1951 indicate

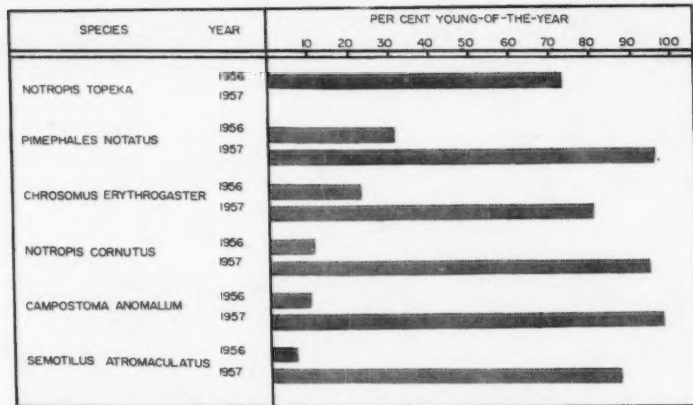


Fig. 2.—Percentage of total population consisting of young-of-the-year, in six species of minnows collected from Deep Creek, Riley County, Kansas, in October, 1956 and December, 1957. Ages were ascertained by the length-frequency method, and checked by examining scales of some individuals. Collections were made from the same pool each year, and checked by collecting in other parts of the stream.

that the Topeka shiner has disappeared from that stream, which is the type locality.

In Wildcat Creek, several records of *N. topeka* have been obtained: by Jennings (1942:365); by Minna Jewell in the 1920's; and by Leonard and Williams in 1947. However, in twenty collections made by Minckley in 1956 and 1957, no Topeka shiners were taken. Only two of the characteristic associates, the creek chub and blunt-nose minnow, were found, and these were scarce. The most abundant species in Minckley's collections from Wildcat Creek were the red shiner, fathead minnow, orangespotted sunfish, black bullhead, and carp (*Cyprinus carpio* Linnaeus). The same species, plus the sand shiner, *Notropis stramineus* (Cope), now prevail at localities west of 97° longitude where *N. topeka* was reported by Gilbert, Cragin, and Hay (*loc. cit.*).

In Rock Creek, series of *N. topeka* were taken by the State Biological Survey in 1912. Recently, only two Topeka shiners (KU 2829) have been collected from Rock Creek (none elsewhere in the Wakarusa drainage). The latter specimens were taken in the headwaters of Rock Creek where it flows through a large area of moderately-grazed grassland.

#### DISCUSSION

According to our concept of the habitat of *N. topeka*, Shunganunga Creek, Wildcat Creek, and Rock Creek are now unsuitable for this species. Flow usually ceases in the spring and the pools that remain become warm and muddy. Bottoms are predominantly mud, and domestic pollution affects parts of Wildcat Creek and Shunganunga Creek. The watersheds of these streams have more cultivated land Creek, the Mill Creeks, and Carnahan Creek. The valleys of the latter streams are narrow, whereas the valleys of Shunganunga Creek, Rock Creek, and Wildcat Creek are relatively broad, accounting for more cultivation and subsequent siltation. All seven of these streams were influenced by the southern extension of the Kansan ice sheet (less, proportionately, in native grasses) than the watersheds of Deep in early Pleistocene (see Mudge, 1955).

Historically, some aspects of the abundance of *N. topeka* in Kansas are indicated by comparison of its past and present distribution in the state (Fig. 1). In the years 1884-1889, reported occurrences of *N. topeka* were exclusively from areas other than the Flint Hills, although collections of other fishes were made in that area by Graham (1885), Cragin (1885), and others. Since that time nearly all records of *N. topeka* have been from streams of the Flint Hills area. In Kansas, it seems that the Topeka shiner has almost disappeared from areas other than the Flint Hills but has increased in abundance in that area. In late years, *N. topeka* seems uncommon during wet cycles, when it occurs primarily in headwater tributaries. During drought, the species is more widespread in the streams, and becomes a much more important part of the Flint Hills fauna.

## CONCLUSIONS

We conclude that, several decades ago, *N. topeka* was most common in prairie streams outside the Flint Hills area. Now the situation is reversed, probably because of changes in climate and agricultural developments. That climate has become warmer in recent decades is evident from weather records and measurements of glacial retreat in colder regions (see Knapp, 1948). The warming trend has caused reduced average run-off and instability of ground-water tables (lowering of the average level), which in turn have caused more frequent intermittency of streams, and higher temperature in residual pools. Cultivation of the prairies almost certainly has augmented these effects, and caused the streams to be more muddy than formerly. Consequently, more streams outside the Flint Hills are now unsuitable for the Topeka shiner.

*Notropis topeka* may have been rare in the Flint Hills Area at the time of settlement because flow in these high-gradient streams (averaging approximately 15 feet per mile) was too great for this species, except in the smaller upland tributaries. Reduced stream-flow in the Flint Hills has allowed populations of the Topeka shiner to increase, primarily because tillage and grazing have not yet caused streams to become temporary, heavily silted, highly turbid, and hot. Agricultural land-use in the Flint Hills has been limited by shallow soils and sharp relief. If agricultural land-use becomes more intensive, the species may decline rather than increase, and extinction may result.

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## Studies on the Alaskan Blackfish *Dallia pectoralis* I. Habitat, Size and Stomach Analyses<sup>1</sup>

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The end-product of evolution via mutation and natural selection frequently results in the establishment of a species well adapted to a limited environment. The distribution of the Alaskan blackfish, *Dallia pectoralis* Bean, limited to arctic and sub-arctic fresh waters, (Jordan and Everman, 1896; Wilimovsky, 1954), suggests that because of modifications necessary for survival in the cold, this species may have become over-specialized, resulting in an organism suitably adapted to the cold. We successfully maintained 50 live blackfish under refrigeration in the laboratory at Catholic University during 1953 and 1954. A second group of 30 animals was kept at room temperature (25°C). The members of this group died within a few weeks even though we attempted to gradually acclimatize them to room temperature.

Other factors suggest that this species is well adapted for survival in the cold. For example, Turner (1886) reports that the Alaskan blackfish was frequently collected by natives, stored in grass baskets, frozen, and fed to dogs. Upon being rewarmed, it is reported, the fish was regurgitated alive by the dogs. Such reports are part of Alaskan folk-lore. Scholander *et. al.* (1953) in an attempt to verify such reports performed critical metabolic and survival studies on the blackfish, the results of which indicated that the fish is, indeed, cold-adapted but it cannot survive freezing.

The above studies suggested to us that an ecological and physiological investigation of the blackfish was warranted. The physiological study will be published separately. The ecological study included determinations of the total alkalinity, pH, dissolved oxygen and temperature of the environment, and of the total length, weight, and stomach contents of the fish. All these factors are interrelated; the physical environment influences the occurrence of food as well as the distribution of the blackfish.

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## MATERIAL AND METHODS

With the Arctic Research Laboratory at Point Barrow, Alaska, as base of operations, collections and field observations were conducted in late July and mid-August, 1955, at Brower's Ranch, "Half Moon Three," about sixty miles southeast of Point Barrow (near  $70^{\circ} 46' N$  and  $155^{\circ} W$ ), between Admiralty Bay on the west and Smith Bay on the east. The area has many tundra lakes and distributary river channels. Tundra polygon formations and permafrost are general over the area.

Dissolved oxygen content was determined by the Rideal-Stewart (Am. Pub. Health Assn., 1941) modification of the Winkler method averaging the results from three 250 ml. samples. La Motte liquid standards graded in 0.2 intervals were used for pH determinations. Total alkalinity was measured by titration with sulfuric acid using methyl red-bromocresol green as an indicator.

The blackfish were collected with a fifteen-foot minnow seine weighted with a heavy metal chain since the aquatic vegetation was quite dense. Even with this gear only repeated hauls with the seine, "wore down" the plants enough to catch the fish. Each station catch for each day was recorded separately.

The weight of the live fish to the nearest 0.1 gm and the total length to the nearest mm were measured within approximately two hours after capture. The fish were then immediately killed, tagged and preserved in formalin for stomach analyses to be performed later in the laboratory.

A modified stratified sampling technique was used in choosing 77 fish for stomach analysis. From each 5 mm-length group at least 20 percent of the fish were used (Fig. 3). Care was taken to make sure that the specimens came from different catches so that at least 20 percent of the fish from each catch were also used (Table II).

## OBSERVATIONS AND RESULTS

## DESCRIPTIONS OF STATIONS

The blackfish were collected from two locations at Half Moon Three: (1) the lake and network of polygon ditches about a hundred yards north of the ranch cabin, and (2) a smaller lake nearly one-half

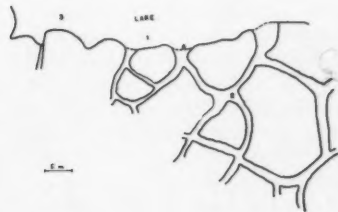


FIG. 1.—Map of edge of lake north of cabin at Half-Moon Three, Alaska. Numbers 1-4 indicate locations of stations where seine hauls were made. Some of the low-lying polygons and their ditches are outlined. Dotted lines indicate a water connection between lake and ditch. Scale is 5 meters to 4 mm.

mile south of the cabin. Although these lakes and polygon ditches appeared similar to others in the area, collection trips to other places proved fruitless.

Stations 1 to 4 (Fig. 1) were located at the southwest edge of the lake and adjacent polygon ditches. The water of the lake within the area indicated by the map was less than 60 cm deep. At Station 3 the water was clear, but from Station 1 eastward, emergent *Arctophila* and submerged vegetation grew quite thickly in places. Both stickleback and blackfish were caught by seine hauls through this vegetation.

The land of northern Alaska typically forms polygons. Next to the lake low polygons covered the area. In the area diagrammed by the map they stood less than a meter above the water level of the lake. Just east of this area, the polygons were marshy in July. As is characteristic of the arctic coastal plain, dense vegetation grew in the few inches of water in the ditches between the polygons. This vegetation, a mixture of emergent grasses and sedges and submergent sphagnum, proved to be the best source of blackfish. Most of the specimens were caught at the "X" formation of ditches at Station 2. It should be noted that no stickleback were taken at this station, and neither stickleback nor blackfish were collected at Station 3.

Station 5 was located in a small pool at the side of the lake south of the cabin. There was a good water connection to the lake through the mixed emergent vegetation. The bottom of the pool was covered with sphagnum. The pool was approximately 6 meters long and the depth at the center was 40 cm. Sixteen blackfish were taken from this pool on August 16.

#### PHYSICAL AND CHEMICAL CONDITIONS OF HABITAT

The results of pH, total alkalinity, and dissolved oxygen analyses are summarized in Table I. In view of the shallowness of the water, samples were collected from the median depth level. Dissolved oxygen, expressed in parts per million (ppm), varied from 2.3 ppm at Station 2 on August 17 to 12.6 ppm at Station 1 on July 29, with a mean of 9.5 ppm. Both of the two lowest readings were made at Station 2 where on July 29 the oxygen content was 8.1 ppm and on August 19 it was 2.3 ppm. In July the mean was 10.5 ppm and in August, 8.7 ppm for Stations 1, 2, 3 and 4. The reading at Station 5 on August 18 was 10.8 ppm.

Note the great variability in total alkalinity and dissolved oxygen with date and station. No reason for this variation was apparent.

The pH readings fell within a relatively narrow range. The highest individual reading was pH 8.0 at Station 1 on August 15, and the lowest reading of 6.8 was noted on three occasions: Station 2 on July 27, Station 2 on July 29 and Station 3 on July 29. The mean for all readings was pH 7.3. Station 2 averaged the lowest for the season with 7.0, and Station 1 had the highest mean, 8.0. Station 3 averaged 7.4; Stations 4 and 5 had identical means of 7.2.

The temperature of the water of the north lake averaged 8.6° C.

TABLE I.—Average readings of chemical and physical environmental factors at the various collecting stations

Station	Date	Dissolved O <sub>2</sub> ppm	pH	Total Alkalinity	Ambient Water T. °C	T. °C
1	July 25-29, 1955	12.6	8.0	121.9	12.2	8.6
	August 15-20, 1955	10.3	7.9	58.0	13.2	7.8
2	July 25-29, 1955	8.1	6.8	212.0	11.6	9.4
	August 15-20, 1955	2.3	7.1	220.0	13.2	7.8
3	July 25-29, 1955	11.1	6.8	60.0	12.2	8.6
	August 15-20, 1955	11.5	7.7	61.2	—	—
4	July 25-29, 1955	—	—	—	—	—
	August 15-20, 1955	4.4	7.2	177.4	—	—
5	July 25-29, 1955	—	—	—	—	—
	August 15-20, 1955	10.8	7.2	53.8	—	—

for July and 7.8° C. for August. The water in the ditches was slightly warmer, 9.4° C. in July and 7.8° C. in August. Ambient temperatures varied more, depending on the weather of the day. The highest ambient temperature reading noted was 13.2° C. and the lowest was slightly above freezing during a snow on August 17.

#### FOOD HABITS

The organisms found in the stomachs of the 77 fish used in the food habit study were grouped into 17 classes (Table II). The highest number of classes found in a single fish stomach was 10 (Station 5, August 16), and the lowest was 0 (Station 1, July 30), with a mean of 5.0 for the total sample. There was some variation between the means for the various stations. The lowest mean for a station was 1.5 classes of organisms per fish for the July catch from Station 1. This station also had the lowest number of classes per catch, 5. The highest mean for a station was 7.0 classes from the August 16 catch from Station 2. In the four catches of July there was a mean of 4.2 classes per fish, whereas the mean from those same stations, Stations 1, 2 and 4, in mid-August stood higher at 5.8. The mean of classes in all fish from Stations 1, 2 and 4 was 5.0.

*Percentage of occurrence of classes.*—The percentage of occurrence of classes is summarized in Fig. 2. For the entire sample the lowest were the alga, *Zygnema*, and fish fry, each with an occurrence of 2.6 percent. Cladocerans were found in 90.9 percent of the fish. Dip- teran larvae and ostracods also appeared with regularity, with a per- centage occurrence of 89.6 and 88.3, respectively. Copepods were found in 62.3 percent and caddis fly larvae in 46.8 percent of the stomachs sampled.

TABLE II.—Mean numbers of organisms found in stomachs of the blackfish

Station	1	2	2	1 & 4	Sub- total	2	1	1 & 4	4	1 & 4	Sub- total	Total Sta. 1-4	Grand total
Date	July 30	July 30	July 31	July 31	July	Aug. 16	Aug. 17	Aug. 17	Aug. 18	Aug. 20	August	July & August	August 16
Fish sampled	4	15	7	10	36	3	1	20	4	6	34	70	77
Nematoda	0.3	0.1	—	0.2	0.1	—	1.0	0.3	—	1.3	0.4	0.3	—
Acanthocephala	—	0.5	1.4	0.6	0.7	1.3	—	0.8	0.3	—	0.6	0.6	0.6
Cladocera	—	6.5	17.7	7.5	8.3	28.7	31.0	21.4	10.5	29.2	22.4	15.1	46.9
Copepoda	0.3	0.2	1.6	1.2	0.8	4.0	2.0	4.7	0.5	1.3	3.4	2.1	18.1
Ostracoda	0.8	16.0	87.6	21.1	33.8	159.3	7.0	37.3	5.9	8.7	38.4	36.0	90.1
Trichoptera	—	—	—	—	—	—	—	—	—	—	—	—	—
larvae	1.0	1.0	0.1	1.0	0.8	3.0	3.0	1.6	0.3	1.0	1.5	1.1	1.1
Diptera larvae	0.5	6.1	11.4	20.9	10.6	11.0	3.0	18.7	25.3	12.3	17.2	13.8	9.0
Diptera adult	—	0.3	0.3	0.4	0.3	—	—	0.1	—	0.2	0.1	0.2	0.3
Hydracarina	—	0.1	—	0.2	0.1	0.3	—	0.1	0.3	—	0.1	0.1	0.6
Physidae	—	0.1	—	0.4	0.1	1.3	—	0.3	0.3	0.3	0.4	0.3	0.2
Planorbidae	—	—	—	0.3	0.1	—	—	0.1	—	0.2	0.1	0.1	—
Fish fry	—	—	—	—	—	1.7	—	—	—	—	0.2	0.1	0.1
Tetraspota	—	0.1	—	—	<0.1	—	—	0.1	—	—	<0.1	<0.1	0.1
Oedogonium	—	—	—	—	—	—	1.0	—	—	—	<0.1	<0.1	1.6
Zygnema	—	—	—	—	—	—	—	—	—	—	—	—	0.3
Nostoc	—	—	0.1	0.2	0.1	0.3	—	0.1	—	—	0.1	0.1	1.9
Other algae	—	0.1	—	—	<0.1	—	—	0.3	—	0.2	0.2	0.1	0.1
No. items per fish	2.8	41.1	120.3	54.4	55.8	211.0	48.0	85.0	43.0	54.7	85.1	70.0	169.3
No. classes per fish	1.5	4.6	4.7	5.4	4.2	7.0	7.0	5.9	4.3	5.7	5.8	5.0	5.6



Differences were noted between the July and August catches. The percentage occurrence for Cladocera, Ostracoda, and Diptera larvae was identical in July, 80.6, with a rise of all three percentages for the August catch to 100, 94.1 and 100, respectively. Nematoda doubled in occurrence in August. Copepods jumped from 44.4 percent in July to 79.4 percent in August. Caddis fly larvae showed an increase of 17.1 percent over July. Snails, too, occurred more frequently in the August catch.

Algae were found more frequently in fish from Station 5 than in those from Stations 1, 2 and 4. Other classes showed no significant variation from the stations at the north lake.

*Numerical occurrence of organisms.*—The total number of individual organisms taken from the 77 stomachs was 6088. The highest number taken from a single fish was 421 and one stomach was empty. Both fish were near the median in length and weight. The mean number of individual organisms per stomach was 79.1 for the entire 77-fish sample. The mean number of organisms per stomach for each catch varied with the station and the date, as well as from fish to fish within each catch. For the four catches taken in July the mean was 55.8. The mean for the same stations increased to 85.1 in August. The fish from the Station 5 catch showed a notably higher mean of 169.3.

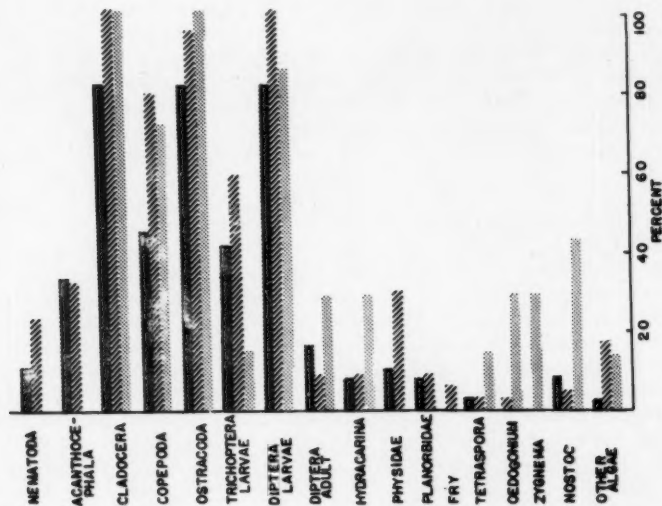


FIG. 2.—Percentage of occurrence of classes of organisms in the stomachs analyzed. The dark bars represent July catches and the cross-hatched bars the August catches from Stations 1, 2, and 4. The dotted bars represent the Station 5 catch.

The catch from Station 1 on July 30, with the average number of 2.8 organisms per stomach, was considerably lower than the next mean, 41.1, from Station 2 on July 30. At the other extreme, the mean number of 211.0 organisms per stomach for Station 2 on August 15 is much higher than the next in order, 169.3 of Station 5 noted above.

*Numerical occurrence of organisms by class.*—If the numbers of individuals by classes of organisms are considered, the ostracods surpassed all other kinds with a total of 3153 of the 6088 items, or 51.8 percent of all individuals identified. The mean number of ostracods per stomach for the entire sample was 41.0. The Cladocera, the next most numerous group, averaged 18.0 individuals per fish, and Diptera larvae was third with a mean of 13.4. With the exception of 1.1 Trichoptera larvae per fish, all other classes averaged less than 1.0 individuals per stomach, and some even less than 0.1.

*Ostracoda.*—The number of individuals of a given class varied from catch to catch. A mean of only 0.8 ostracods was found in stomachs sampled from the Station 1, July 30 catch. The highest mean number of ostracods was 159.3 per stomach for the fish caught at Station 2 on August 16. There was only a slight variation in the mean number of ostracods between the July and August catches. The mean for July was 33.8 and for August it was 38.4. For the Station 5 catch, not listed above in the mean for August, ostracods averaged 90.1 per fish, the second highest listing for all stations.

*Cladocera.*—The mean number of cladocerans from Stations 1, 2 and 4 for July was 8.3, considerably less than the mean for August, 22.4. And, with one exception, 10.5 for Station 4, August 18, all catches of August had a higher mean number of cladocerans per fish than any July catch. The Station 5 catch had a mean of 46.9, which was notably higher than the next largest, 29.2 (Station 1 and 4, August 20). Variation in means for July was from 0.0 to 17.7, and for August at Stations 1, 2 and 4 from 10.5 to 28.2.

*Diptera larvae.*—The mean number of 17.2 dipteran larvae per fish for the August catches from Stations 1, 2 and 4 considerably exceeded the mean of 10.6 for the July catches. In the July catch six fish stomachs contained no dipteran larvae. At the other extreme, 90 larvae were removed from a fish of the July 31, Station 1 and 4 catch. Less variation was noted in the fish captured from those same stations in August. Two stomachs had a single larva and one reached the maximum counted, 73 larvae. This latter fish was the one noted previously as having 421 organisms in the stomach. The catches in July varied from 0.5 to 20.9 larvae, whereas the August catches from the same stations averaged from 11.0 to 25.3 larvae per stomach. The fish from Station 5 had a mean of 9.0 dipteran larvae per stomach.

*Copepoda.*—There was an average of 3.4 copepods per fish for the total sample. Fish from Stations 1, 2 and 4 had a mean of 0.7 for July and 3.4 for August. A mean of 18.1 copepods, however, was found in the fish from Station 5. In this catch the largest number, found in two stomachs, was 37 and the lowest number was 10. The

next highest mean for a station catch was 4.6 copepods (Stations 1 and 4, August 17). The range was from 0 to 23. The range of mean numbers of copepods per fish for individual catches from Stations 1, 2 and 4 in July was from 0.3 for Station 1 on July 30 to 1.6 for Station 2 on July 31. For the same stations the range in August was from 0.5 for Station 4 to 4.7 per fish from Stations 1 and 4 on August 17.

Other.—The only other class with an average of more than one individual per fish was the Trichoptera larvae with a mean of 1.1. The mean of Stations 1, 2 and 4 was 0.8 in July and 1.12 in August. At Station 5 the mean was 0.3. The catch with the highest mean of caddis fly larvae per stomach, 3.0, was taken from Station 2 on August 17; that with the lowest mean, 0.1, came from the same station on July 31. All other classes averaged less than one individual per fish not only for the total and July and August subtotals, but also for each station catch with the following exceptions: Acanthocephala for Station 2, July 31 with a mean of 1.4 and August 16 with a mean of 1.3; Physidae for Station 2, August 16, with a mean of 1.3; and fish fry in the stomachs of fish from Station 2, August 16 with a mean of 1.7.

#### LENGTH AND WEIGHT

The mean total length of all 256 fish was 71.7 mm. The median was 72 mm. Two fish measured 30 mm and one was 116 mm long. There were less than 10 fish in each 5 mm group below 60 mm and above 90 mm. There were 201 fish within the 60-90 mm range. The highest number of fish in a 5 mm group within this range was 56 for

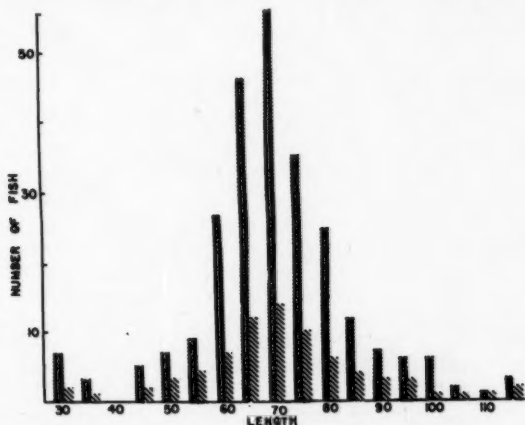


FIG. 3.—Distribution of fish according to 5 mm length groups. The dark bars represent the total number of fish in each group and the cross-hatched bars represent the number of fish used for stomach analyses from each group.

the 70-74 mm group, and the lowest number was 12 fish in the 85-89 mm group (Fig. 3).

The mean weight of all fish was 4.09 gm and the median weight was 3.8 gm. Two fish weighed 0.2 gm and one weighed 14.4 gm. There were fewer than 10 fish in each 0.5 gm group below 1.5 gm and above 6.0 gm. Within the 1.5-5.9 mm range there were 201 fish. The 2.5-2.9 group and the 3.0-3.4 gm group each had 32 fish; the 1.0-1.4 gm group contained 10 fish.

Individual fish of identical length varied in weight and vice versa (Fig. 4). The group of 13 fish measuring 70 mm each showed considerable variation. Their weight varied from 2.8 gm to 5.2 gm with a mean weight of 3.49 gm. Other groups had a smaller weight range.

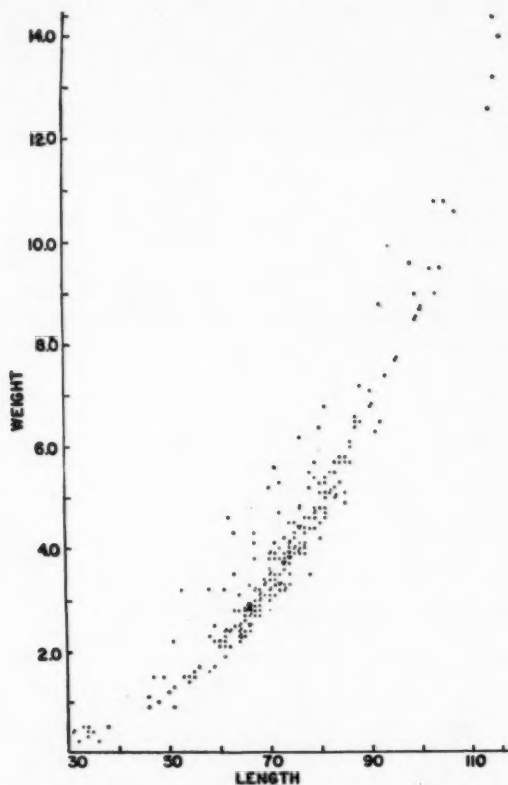


FIG. 4.—Length-weight relationship. Live total length is expressed in mm and weight in grams. Each dot represents one of the 256 fish captured.

Individual fish of a certain weight varied in length. The 12 fish weighing 2.8 gm each had a total length range from 63 mm to 70 mm. A spread of 15 mm, 58-73 mm, was noted in the 10 fish weighing 3.2 gm.

## DISCUSSION

### HABITAT

Jordan and Evermann (1896) noted that the blackfish is found in streams and abounds in sphagnum ponds "wherever there is water enough to wet the skin of a fish." It has also been given the name of "grassfish." The present study supports these popular concepts. The blackfish were caught in dense aquatic vegetation of the lake edges and polygon ditches. None were seen or captured in the clear water of the lake. It cannot be concluded from this study that blackfish can be found in many such habitat locations in northern Alaska. Hauls were made in other ditches and tundra ponds with an evident water connection to the same lake, and with the same general appearance as the stations used, but no blackfish were captured. No explanation for this rather limited distribution at Brower's Ranch can be offered at the present time.

The blackfish is apparently able to tolerate crowding from its own kind, as well as competition from other fish. The volume of water in the polygon ditches was quite small in view of the number of fish captured. In addition to blackfish, approximately 150 stickleback were also seined from Stations 1 and 4. The physical aspects of the environment that were measured at Station 3 were similar to those recorded from other stations. Despite this physical similarity, blackfish were not present at Station 3, but were present at other stations. Station 3, because of the lack of rooted vegetation, afforded no means of concealment for the fish.

A large number of blackfish were found in water with a dissolved oxygen content of 2.30 ppm. This is indicative of the organism's ability to tolerate an environment low in oxygen. Moore (1942) studied the effect of oxygen tension on the survival of eight species of fish in Minnesota lakes. He found that the minimal dissolved oxygen limit is related to the water temperature. At 15-26° C a dissolved oxygen content of 5 ppm is adequate, while a content of 3.5 ppm is lethal. At 0-4° C the minimal need is only 2 ppm. The need for a high dissolved oxygen tension at high temperatures is related to the metabolic rate of the organism. However, unlike many temperate zone species, the blackfish is active at temperatures as low as 4° C (Nardone, 1954). The survival of an active organism despite low oxygen tensions is related to the low  $Q_{10}$  for tissue respiration, and to the utilization of metabolic pathways that are not highly aerobic (Hanzely, 1955).

Regarding other habitat conditions it should be noted that the pH range of the water found in this investigation was similar to the findings in other waters of the Arctic Coastal Plain (Prescott, 1953). The

lack of a correlation between oxygen tension, pH, and temperature cannot be accounted for.

#### FOOD HABITS

Jordan and Evermann (1896) state that the blackfish feeds on plants and worms. The data obtained in the present study does not substantiate this statement since plants and worms formed only a small percentage of the total stomach contents. Cladocerans, ostracods and dipteran larvae were far more numerous (Table II). Cladocera occurred in the greatest number of stomachs. This was not significant because the percent occurrence was only slightly above the percent occurrence of Ostracoda and of the dipteran larvae. The number of cladocerans per stomach, moreover, was the lowest of these three classes. More ostracods than all other classes combined were found in the stomachs sampled. Their relatively small size and resistance to digestion, however, lessens to some extent, the importance to be attached to them as food organisms. Dipteran larvae, on the other hand, were the largest in size individually and readily digestible. The indication is, therefore, that the dipteran larvae was the most important class of food in the fish sampled in this investigation.

Whether or not all classes of organisms found in the stomach were eaten by the fish as food cannot be definitely stated. The occurrence of fish fry, for example, in two stomachs may indicate a cannibalistic feeding habit. On the other hand, the adults could have swallowed the fry accidentally while feeding. Another case in point is that of *Acanthocephala*, found in many stomachs. Their presence can be explained in several ways. One is that they are parasites of the fish that have not yet become attached, or were detached from the stomach wall in the process of dissecting and emptying the stomach. These parasites are known to exist in such invertebrate hosts as Ostracoda (Hoff, 1942). Thus they may have been ingested as parasites of ostracods. In all stomachs in which *Acanthocephala* was present ostracods were also found, but not vice versa.

The main classes of food seemed to form the bulk of the diet for fish of all sizes from all stations without significant change between the times of catching. No definite pattern of variation could be formed, with one minor exception. Caddis fly larvae were found only in stomachs of fish whose total length exceeded 58 mm. The number of organisms varied from fish to fish, but also without a definite pattern of variation. The small number of individual organisms found in the fish from Station 1, July 31, can perhaps be explained by the fact that the blackfish were killed about three hours after capture, whereas on subsequent occasions the fish were killed more promptly. The lack of a comprehensive study of the life cycles of these invertebrate species in Alaska makes it impossible to evaluate how much importance should be attached to the differences between the July and August samples.



## LENGTH-WEIGHT

The length-weight relationship of the blackfish caught at Half Moon Three is recorded in Figure 4 and indicates their pattern of growth. Although the data comes from only 256 fish, the results are similar to those of Hile (1936) and Beckman (1948).

## SUMMARY

A study of some aspects of the ecology of the arctic blackfish, *Dallia pectoralis*, was made. Ecological studies included pH, alkalinity, temperature, oxygen content of the water, and feeding characteristics of the fish.

The pH of the water ranged from pH 6.8 to 8.0. Water temperature varied from 7.8° C to 13.2° C. Dissolved oxygen varied from 2.30 to 12.58 ppm. Ostracoda, Cladocera and larvae of Diptera were the principle food organisms, in number and frequency of occurrence. There was, however, great variability from specimen to specimen.

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## A Historical View of the Ranges of the White-Tailed Deer in Northern Wisconsin Forests<sup>1</sup>

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The original forests of northern Wisconsin were largely mixed conifer-hardwoods. The vegetational maps of Chamberlin (1882) and Curtis (1950) indicate the horizontal distribution of the mixed conifer-hardwoods. The swamp distribution maps of Huels (1915) and Fuller (1933) show the extent of swamps. The history of the ranges of the white-tailed deer in northern Wisconsin may be reviewed in the light of the distribution of native vegetation, subsequent vegetational changes, and the trends in the deer population.

Several papers have dealt with the history of Wisconsin deer populations (Swift, 1946; Schorger, 1953; Guettinger and Dahlberg, in prep.). These studies indicate that deer populations in northern Wisconsin were relatively low prior to 1850, that the deer population increased until the late part of the 19th century, that the herd then underwent a decline to the 1920's, and that the highest population levels were reached in the late 1940's. These deer population trends, and the accompanying changes in forest vegetation, have not been specifically studied with regard to winter and summer habitat requirements of the white-tailed deer.

The lowland forests (exclusive of the tamarack-black spruce bogs) are generally the most productive winter deer ranges and they are more generally used as winter habitats by white-tailed deer than are the upland forests. In evaluating historical accounts of the vegetation it is assumed that the swamp forests (especially white cedar swamps) represent the winter range lands that best meet the requirements of the deer in the past. The upland forests were summer range generally. Upland young white pine and hemlock forests presumably meet the winter cover requirements of deer, and might be considered as winter range, but it is doubtful if the mature forests of the original upland vegetation could have supported a very sizable deer population in either summer or winter. Especially is this true of the mature white pine forests.

### SUMMER RANGE — HISTORICAL INFORMATION

Several descriptions are available which indicate that many upland mixed conifer-hardwood forests were doubtless summer ranges with low carrying capacity for deer. The conclusion can be drawn from the following that much of the upland area of northern Wis-

<sup>1</sup> Financial aid was provided by the Game Research Division, Wisconsin Conservation Department.

consin was characterized by mature forests with little undergrowth, conditions indicative of low carrying capacity. Irving (1880) wrote concerning the vegetation of northern Ashland and Bayfield counties: "The maple trees are generally of much larger size than those of the evergreen varieties, and where they grow there is less undergrowth . . ." Concerning northern Douglas and Bayfield counties, the following was written by Sweet (1880): "In the eastern part . . . hemlock is the prevailing growth . . . The hemlock trees are usually from one to three feet in diameter, and stand quite close together."

Historical records indicate that large areas in northern Wisconsin were essentially monotypes of vegetation. Bartlett (1938), Swift (1946) and Guettinger and Dahlberg (in prep.) have indicated that large areas of any one species, or any one cover type, cannot support a very large deer population. Roth (1898) wrote: "In the regular pinery of the sandy soils the pines predominated, the hemlock was entirely wanting and the hardwoods were scantily represented by small white birch, aspen, and maple, which were mixed with the young pine." Roth also described the southern three-fourths of Vilas County as an "uninterrupted pinery, principally white pine with little Norway and hardly any jack pine."

Cram (1841) reported that the "country adjacent to the upper part of the Menomonee, for about thirty miles on both sides . . . has been consumed by fires . . . studded here and there with charred pine stubs, with scarcely a living tree, except the second growth of white birch and poplar."

The observations of Norwood (1852) also indicate low and moderate productivity of the summer range of Vilas County. Norwood made the following observations about the upland vegetation of parts of Vilas County:

"The soil is thin but supports a growth of small pine, poplar, birch, spruce, hemlock, and fir, a few oaks, and some bass-wood. . ."

"The high and broad strip of land which divides the waters of the Chipewewa from those of the Wisconsin is made up of white sand, with small boulders thinly scattered over the surface. The pines with which it is covered are small, but very tall and straight, many of their trunks rising fifty or sixty feet without a branch. On some of the higher hills a great many small birch were seen; and in the vicinity of Muscle Lake the sugar maple began to appear."

"Trout Lake . . . is surrounded by drift hills . . . supporting a sparse growth of small pines and birch."

"A narrow strip of small pines lines the banks of the river at intervals: but, as you recede into the country, there are few trees of any size to be seen. Clumps of very small birch and pines are scattered over it."

The banks of the Wisconsin River "are from three to twenty feet high, and covered with pine, fir, and spruce, with a few aspens and small birch."

"The country for a short distance above and opposite these rapids is open, bearing thickets or small birch, and a few stunted pines scattered through them. Occasionally, a solitary large pine was seen standing on a sandy knoll, twenty

or thirty feet above the level of the river. Below the last rapids the country is . . . supporting a tolerably good growth of pine, birch, and aspen."

Norwood also described an area in the southeastern corner of Iron County.

"The trail runs over a sand barren, with the exception of the last half mile, which passes through one of the worst tamarack swamps I have ever seen. A few stunted pines, with occasional patches of coarse grass, is the only vegetation supported on the high grounds."

Some of the original broadleaf forests were good summer range as is indicated by the following description of the original hardwood forest by Roth (1898): "In almost all parts of the mixed forest of the loam lands, the hardwoods formed the body of the forest and the conifers the admixture. The hardwoods were represented by trees of all sizes, from the seedling or sprout to the mature timber tree. They formed nearly all of the undergrowth and this hardwood forest showed every indication of thrift and permanence." Chamberlin (1877) observed the following about the understory of the "Hardwood and Conifer Group": "The Ironwood is far less abundant . . . the Witch Hazel (*Hamamelis Virginica*), and the Mountain Maple (*Acer spicatum*) appear more prominently among the underbrush. The berry-bearing plants are multiplied . . ."

#### WINTER DEER POPULATIONS AND SEASONAL MOVEMENTS OF THE WHITE-TAILED DEER

Historical records indicate that the white-tailed deer wintered in much the same areas in northern Wisconsin as they do today. Schorger (1953) noted that the belief existed a century ago that deer migrated southward in winter from northern Wisconsin. However, after reviewing the sources of the belief he draws the following conclusion: "There is no authentic information to support the statements that formerly there was a migration of deer. . . . The local disappearance of deer was usually due to yarding."

There is considerable historical evidence that deer wintered in northern Wisconsin in yards, especially in lowland areas. Schorger refers to several papers from which evidence of winter range use is presented. Fonda (1868) frequently found herds of deer that had yarded in "heavily timbered bottoms" in the winter of 1827-28 between Green Bay and Chicago. Curot (1911) purchased deer at his post on the Yellow River, Burnett County, during the winter of 1803-04. Allen (1834) stated, after an observation in 1832, that the Indians kill large numbers of deer in fall and winter along the Chippewa River. Schorger points out: "It is possible that the Indians, to obtain deer in quantity, descended the Flambeau River [from Lac du Flambeau] to its junction with the Chippewa in extreme southern Rusk County." Hough (1895) was told that deer wintered in a heavy thicket in the vicinity of big St. Germain Lake, Vilas County.

Cram (1841) wrote that the valley of the Menominee had deer in great abundance and was a favorite winter hunting ground for Indians from various quarters.

Schorger (1953) cites many winters during the period 1661 to 1888 when the conditions were severe enough to produce local starvation and reduction of the deer population in various areas throughout northern Wisconsin. These data were gathered by an extensive search of historical publications including books, journals, newspapers and other writings. Significantly, the first definite mention of deer in Wisconsin was by Radisson (1888) who described winter starvation conditions in northwestern Wisconsin during the winter of 1661-62. Concerning the "small staggs" he stated: "It's an easy matter for us to take them out and cutt their throats with our knives." It is certain that locally in some years, the deer population exceeded the carrying capacity of the winter range in northern Wisconsin, and that this occurred even when the deer population was small in comparison with that of recent years.

#### WINTER RANGE — HISTORICAL INFORMATION

The dense canopy cover and heavy undergrowth pointed out in the descriptions of the swamp forests of northern Wisconsin indicate good winter range conditions. Roth (1898) wrote:

"The greater part of the swamps in Northern Wisconsin were well stocked with dense thickets of tamarack, cedar (*arborvitae*), and scattering spruce. The cedar (*arborvitae*) prevailed in those of the eastern part, especially the swamps of the sandy loam lands along and near Green Bay, the tamarack had undisputed possession of those of the southern and southwestern part and also covered part of the swamps of the openings. The swamps of the central, northern, and northwestern part were stocked without regularity, some with tamarack, others with cedar, and in many of them both trees occurred together. The spruce as a very runty shrub or half tree covered many open bogs and otherwise occurred scattered in the swamps, especially within the moister hemlock area."

Irving (1880) noted the following concerning northern Bayfield and Ashland lowlands:

"The prevailing trees of the district are of evergreen varieties. In the lowland areas north of the Copper Range, the prevailing growth noticed was of balsam, hemlock, spruce and birch, with some white cedar and occasional areas of pine, or scattering pine trees. . . In the swampy region south of the Iron Range, the timber is mostly balsam, cedar, spruce and tamarack of small size, with scattering large pine trees and occasional tracts of white pine."

" . . Besides these true swamps there are other areas hardly wet enough to be so called, which yet support a more or less distinctly swamp timber growth, chiefly of cedar."

" . . So dense is the timber growth that not only is traveling rendered to the last degree difficult, foot traveling being the only kind possible, but it is a rare thing that one can see more than a few rods, or attain a point of observation from which any wide view . . . can be obtained. The traveling is ren-

dered yet more difficult by the frequent areas of fallen timber, known as 'windfalls.'"

Sweet (1880) made the following observations about northern Douglas and Bayfield counties:

"... The explorer is subject to the incessant annoyance of having to clamber over the trunks of fallen trees, or to grope his way through dense thickets of underbrush, or wade through nearly impassable swamps of cedar."

"Along the lake shore in Douglas County and extending into Bayfield County, and reaching back as far as the Copper Range, there is a very dense growth of small trees consisting of about equal numbers of poplar, birch, cedar and balsam. These trees are ordinarily less than a foot in diameter, and from twenty to eighty feet in height."

"To the south and southwest of the Copper Range there is a large tract of country occupied mainly by dense swamps of cedar and tamarac. The trees are small, generally going from six to ten inches in diameter, and often so close together that it is with great difficulty that a person can pass between them. In the swamps, and associated with the cedar and tamarac, are often found balsam and spruce."

As common shrub in the swamps, Sweet listed Kinnikinnik, Red-osier, and Huckleberry.

Strong (1880) wrote about the swamps of Polk and Burnett counties and the adjacent parts of the surrounding counties: "The conifer swamps are either an almost impenetrable jungle of white cedar, or are covered with tamarac and spruce."

Concerning the Lac Vieux Desert, Vilas County, Cram (1841) observed:

"The growth of timber is tolerably heavy, consisting of white and yellow pine on the borders of the lakes; in some instances of cedar, fir, hemlock, and tamarack."

He had this to say about the Brule River, Michigan:

"The banks of the Brule . . . are thickly studded with white cedar, fir, poplar, tamarack, white birch, and pine, for a great portion of its extent. So dense is the growth of timber immediately on the banks, that it is very difficult for one to work his way through it; and for many miles the cedars overhang the river from both sides, so as to lap by each other, and there is barely room under the leaning trunks for the passage of a canoe."

Marked differences in the carrying capacity exhibited by different lowland areas in early Wisconsin are illustrated by King's (1882) comparison of the swamp vegetation (1873-1879) of the Upper Lake Region (Vilas County, generally) and the Lower Valley (Price County, generally) of the Upper Flambeau Valley. Tamarack bogs are not used to any extent as winter ranges, but white Cedar swamps are used universally. King pointed out: "White cedar in the swamps of the latter [lower valley] are replaced by stunted tamaracks in those of the former [upper valley] . . . Many of the small, open swamps in the Upper Lake Region bear a few cranberries . . ." Norwood



(1852) described the lowlands of Vilas County: "... the swamps, as usual, being filled with tamarack, or where that is wanting, overrun with cranberry bushes." "The low grounds . . . support elm, and, where very low, tamarack in abundance." In addition, King stated that the spruce and balsam were abundant and vigorous in the Lower Valley. Black alder and kinnickinnic fringed the streams throughout the Upper Flambeau Valley, and upon some of the flats, small black ash, elm and soft maple grew.

#### DISCUSSION

The historical references to the vegetation point out the fact that the winter range was adequate to sustain at least the deer populations that were present in Wisconsin before the advent of logging. It has been shown that the white-tailed deer were using swamps as winter range from the earliest times for which historical records are available.

The historical references to the lowlands further indicate that the vegetation was generally in excellent condition from the standpoint of winter range. The canopies were dense and the shrubby browse species occurred commonly. The white-tailed deer were a part of these lowland communities. The browsing pressure from Wisconsin's historical deer herd was a natural part of the ecology of the lowland communities. Around the beginning of the 20th century, however, the stability of the communities was upset by two primary factors: destruction of the lowland ranges and expanding deer herds.

It is generally believed that the mature upland forests were capable of sustaining only low deer populations either in summer or winter. The historical evidence here presented gives credence to this belief. The original uncut forests were especially poor winter ranges. After logging began, the cut-over areas became fine summer ranges, at least temporarily, as the early stages of forest development took place.

A summary of the changes that occurred in Wisconsin's deer ranges after the exploitation of the forests began follows: The pines were cut first. The winter ranges in the lowlands were but little abused, and thus, the winter range conditions were not materially altered. As the white pines were cut, sapling hardwoods and shrubby browse species increased in abundance and very favorable summer range was created. In some instances the white pine reproduced and the dense young trees were available for summer and winter range.

According to Roth (1898), toward the late 1800's the swamps of every northern county had shown some effects from fires which resulted from the logging operations. The swamps of Oneida, Price, Chippewa, and Marinette counties had been the site of several fires. Some cutting on a small scale was done in the conifer swamps, and some swamps were drying up or being drained. However, the winter range apparently was still adequate to sustain the deer population which had increased by this time as a result of favorable summer range conditions.

After 1900, the hemlocks were cut in greater quantity. The swamps were cut, burned, and drained during the forest exploitation. By 1920, most of the hemlock and hardwood forests were felled. This reduction in deer winter range was not noticed because it coincided with the low point of the deer population, the result, primarily, of excessive hunting pressure. With continued cutting of the hemlocks and hardwoods, the regrowth of these forests, and their protection from fire, especially since 1930 (Mitchell and LeMay, 1952), a favorable summer range has been developing. However, the deer population increased generally throughout the state with protection, and by the 1930's it was evident that the reduced winter range would not be capable of sustaining the rapidly growing deer population for long (Scott, 1938; Hammerstrom and Blake, 1939; Minor and Hansen, 1939; Feeney, 1942, 1943; Leopold, 1943; Citizens' Deer Committee, 1943).

During the late 1940's overbrowsing in northern Wisconsin ranges was almost universal, with the exception of the Indian Reservations (Swift, 1946; DeBoer, 1947; Leopold, 1946, 1947; Leopold, *et al.*, 1947; Dahlberg, 1949; Dahlberg and Guettinger, 1949; Stollberg, 1949; Hein, 1949; Martin and Krefting, 1953; Guettinger and Dahlberg, in prep.). A consideration of the population trends of white-tailed deer, the history of vegetation change, and the current situation on the winter ranges leads one to believe that the relation of summer to winter range in terms of area and carrying capacity has always been a factor limiting the deer population. It is evident that the winter range will remain the limiting factor for some time to come.

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## Entocythere neglecta sp. nov., a Cytherid Ostracod Commensal on Pacifastacus nigrescens (Stimpson)

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Up to the present time, four species of commensal cytherid ostracods have been described from crayfishes of the western United States. Two of these, *Entocythere columbia* Dobbin (1941) and *E. occidentalis* Kozloff and Whitman (1954), have been taken from hosts referable to *Pacifastacus leniusculus* (Dana), *P. trowbridgii* (Stimpson), and *P. klamathensis* (Stimpson).<sup>1</sup> The other two species, *E. caudata* Kozloff and *E. ericksoni* Kozloff (1955), were found on *P. gambelii* (Girard).

Through the courtesy of Dr. Elisabeth Deichmann, Museum of Comparative Zoology, Harvard University, and Dr. Fenner A. Chace, Jr., United States National Museum, we have had the privilege of studying the ostracods associated with *P. nigrescens* (Stimpson). The ostracods found on this crayfish belong to a previously undescribed species, for which we propose the name *Entocythere neglecta*.

Four collections of *P. nigrescens* provided the material for our investigation. One series (MCZ No. 3390), presented by Dr. F. Steindachner, is said to have been collected at San Francisco, California; it was received by the Museum of Comparative Zoology in 1873, but the exact date of collection has not been established. Another specimen (USNM No. 4974), consigned to the United States National Museum by the Museum of Comparative Zoology in 1883, was possibly taken from the series donated by Dr. Steindachner. Two other series of *P. nigrescens* (MCZ Nos. 228, 3369), also collected at San Francisco, and presented to the Museum of Comparative Zoology by T. G. Cary (no date), likewise yielded commensal ostracods.

Unfortunately, crayfishes referable to *P. nigrescens* seem not to have been collected for many years. The type series, taken at San Francisco (where *P. nigrescens* is said to have been common) is thought to have been destroyed in the Chicago fire of 1871. Single specimens from Fort Steilacoom, Washington (USNM No. 2256) and from Unalaska (USNM No. 8954) appear to constitute the only museum material of *P. nigrescens* from specific localities other than the vicinity of San Francisco.

The specimens of *P. nigrescens* from which *E. neglecta* was taken had been stored in alcohol. The ostracods were found primarily among the cuticular hairs on the ventral side of the thorax and among the

<sup>1</sup> Bott (1950) has proposed the genus *Pacifastacus* to include the several species of North American crayfishes formerly assigned to *Astacus*.

mouth parts of the hosts. For permanent preparations the specimens were dehydrated in ethyl alcohol, cleared in toluol, and mounted in Harleco synthetic resin or in Canada balsam.

*Entocythere neglecta* sp. nov.

(Figs. 1-14)

*Male*.—The valves of the shell (Fig. 1) are smoothly rounded on the dorsal and anterior margins. The posterior margin shows only a slight curvature. The ventral margin is nearly straight, but exhibits a shallow concavity in the anterior half. The height of the shell is greatest a short distance posterior to the middle. In twenty-two specimens, the length of the shell ranged from .39 mm to .42 mm, and the height ranged from .22 mm to .25 mm. There are a number of minute bristles scattered on the outside surfaces of the valves, near the margins. The median eye is heavily pigmented and is situated about one-fifth of the way from the anterior margin of the body; as seen from the side, it is round to oval in outline.

The antennules (Fig. 5) are composed of six podomeres. There is one seta on the first podomere and one on the second, two setae on the third, six on the fourth, none on the fifth, and five terminal setae on the last podomere.

The antennae (Fig. 6) are composed of four podomeres, the third of which is divided. The basal podomere has a long flagellum-like exopodite. The second podomere has one seta. The proximal division of the third podomere bears two setae of approximately equal length, and the distal division bears a single seta. There are three terminal claws on the small fourth podomere. The ventral claw is slightly longer than the dorsal claw, but lacks the distinctly demarcated, flattened terminal portion of the latter; the middle claw is about one-half the length of the other claws. Each claw is provided with sharp, comb-like teeth, which, except for the most anterior tooth, are arranged in two parallel series directed away from one another. If the claws are viewed from the side, it may appear to the observer that there is only one row of teeth.

The distal end of the protopodite of the mandible (Fig. 9) has six teeth. The distal tooth is wider than the others and has five cusps; the remaining five teeth all appear to have three cusps. The convex surface of the protopodite bears a single seta. The distal podomere of the mandibular palp is sharply demarcated, but the rest of the palp is not segmented. There is a long seta on the flexor side of the undivided basal portion. There are two setae close to the distal end of the basal portion; one of them is on the extensor side, the other is lateral and somewhat proximal to the first. The distal podomere bears a heavy spine-like seta and two shorter bristles. The respiratory plate of the mandible is represented by three long setae.

The protopodite of the maxilla (Fig. 10) bears two long setae. The palp is unsegmented and terminates in two curved setae; the



more ventral of these is relatively heavy and dorsoventrally flattened.

The three pairs of thoracic legs (Fig. 11) are similar, with the legs of each successive pair being slightly longer than the preceding pair. Each leg is composed of four podomeres. There are two setae, one of which is about twice as long as the other, arising from the anterodistal corner of the first podomere of the first leg. On the second and third legs, there is a single seta in this position. There is one seta on the second podomere, and a short, minutely hirsute seta on the third podomere. The terminal claw has five teeth.

The basal piece of the copulatory complex (Fig. 13) consists of a broad proximal portion, from which the clasping apparatus and the ventral and dorsal fingers originate, and a more narrow distal portion. The spine at the tip of the ventral finger extends beyond the end of the basal piece. The dorsal finger and its proportionately long spine together have a length slightly less than one-half that of the ventral finger. The distal end of the basal piece has a deep incision, bordered dorsally by a spine-like process, and ventrally by a more substantial projection. This ventral projection is rather evenly rounded distally, and bears a tooth on its upper margin close to the tip. The clasping apparatus (Fig. 14) is nearly C-shaped, its outer edge being rather smoothly curved. The tip of the clasping apparatus is divided into five distinct teeth. There are three teeth on the inner border of the distal half of the clasping apparatus. The most nearly distal of these teeth is the smallest, and the most nearly proximal tooth is the largest.

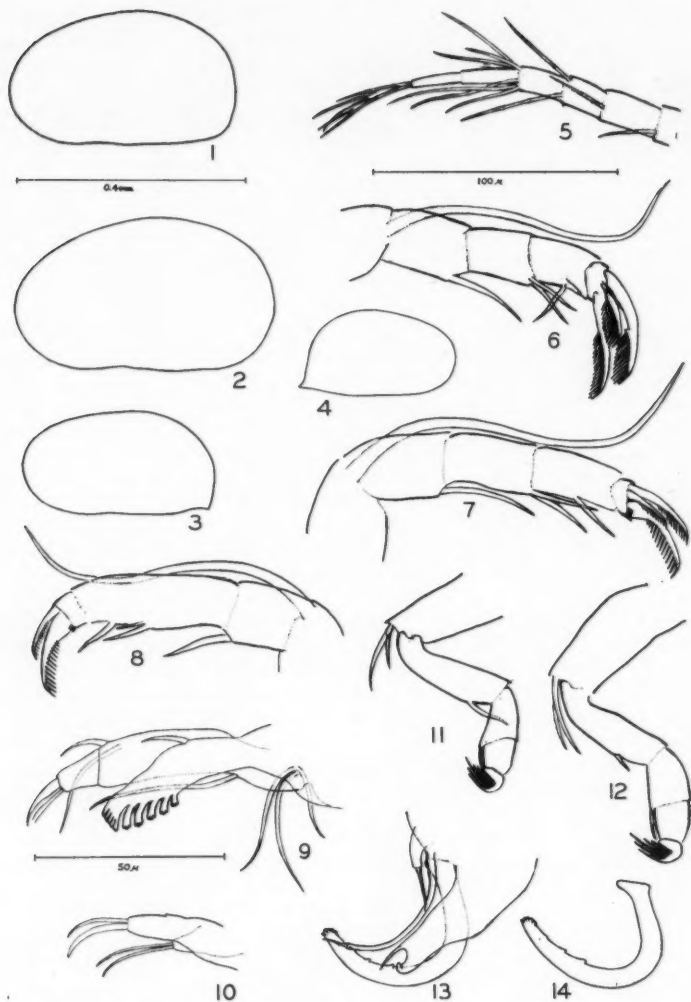
*Female*.—The posterior margin of the shell of the gravid female (Fig. 2) is more conspicuously rounded than in the male, and the concavity in the ventral margin is more pronounced, but in other respects the shells are similar. In forty-two gravid females the length ranged from .36 mm to .49 mm, and the height ranged from .20 mm to .31 mm.

In the copulating female (Fig. 3), the posterior and ventral margins come together to form a rather sharp point. The shells of thirty-four copulating females ranged in length from .34 mm to .43 mm, and in height from .19 mm to .25 mm.

The antennules of the gravid female resemble those of the male. The antennae of the two sexes are different in that the dorsal claw of the antenna of the gravid female (Fig. 7) tapers gradually from its base, instead of having the distal half sharply differentiated from the proximal half as is the case in the male. There is a small comb-like structure projecting from the distal podomere near the base of the ventral claw.

The mandibles and maxillae of the gravid female are like those of the male. The thoracic legs of the female (Fig. 12) also resemble those of the male, but the two setae on the first podomere of the first leg are of approximately the same length.

In copulating females, the penultimate podomere of the antenna (Fig. 8) is undivided, and bears a single seta, which corresponds to



Figs. 1-14.—*Entocythere neglecta* sp. nov. 1.—Left valve of male. 2.—Left valve of gravid female. 3.—Left valve of copulating female. 4.—Right valve of juvenile. 5.—Lateral view of left antennule of male. 6.—Medial view of left antenna of male. 7.—Medial view of left antenna of gravid female. 8.—Medial view of right antenna of copulating female. 9.—Medial view of right mandible of male. 10.—Lateral view of left maxilla of male. 11.—Lateral view of left first thoracic leg of male. 12.—Medial view of right

the one arising from the distal division of the podomere in the gravid female. There are only two terminal claws on the antenna of the copulating female. The comb-like structure found in the distal podomere of the antenna of the gravid female is represented also in the copulating female. The other appendages of the copulating female are similar to those of the gravid female.

*Juvenile*.—The valves of the shell in juvenile specimens (Fig. 4) are distinctly different from those of mature individuals in having a conspicuous sharp projection at the posterior end. Juveniles of *E. neglecta* therefore bear a superficial resemblance to mature examples of *E. caudata*.

*Type specimens*.—The holotype (male), allotype (gravid female), and five paratypes (two copulating pairs, one juvenile) have been deposited in the Museum of Comparative Zoology, Harvard University (MCZ No. 126676). These were taken from *Pacifastacus nigrescens* (Stimpson) collected at San Francisco, California (MCZ No. 3390, presented to the Museum of Comparative Zoology by Dr. F. Steindachner, 1873). Three paratypes (one copulating pair, one gravid female) taken from the same series of crayfish have been deposited in the United States National Museum (USNM No. 102106).

*Remarks*.—*Entocythere neglecta*, although clearly distinct from any other known species of the genus, appears to be rather closely related to certain of the species previously described from western crayfishes. The form of the clasping apparatus and the dentition of this structure in *E. neglecta* are perhaps most nearly like those of *E. ericksoni* Kozloff (1955). The deep incision in the distal portion of the basal piece of the copulatory complex is also somewhat similar in these two species. The valves of the shell in males of *E. neglecta* are quite different from those of *E. ericksoni*, although the shells of the gravid females of these two species are similar. There is a striking difference, however, in the case of the shells of copulating females of *E. neglecta* and *E. ericksoni*.

In connection with this description of a new species of *Entocythere* from typical *P. nigrescens*, we wish to record some information concerning the ostracods associated with *P. nigrescens* subsp. *fortis* Faxon. Crayfishes referable to this subspecies were originally collected at two localities in Shasta County, California: at Fall River Mills (where the Fall River joins the Pit River), and at Cassel (in Hat Creek, which flows into the Pit River). Both series, each consisting of only a few specimens, are in the United States National Museum (USNM Nos. 44404, 44405). We failed to find ostracods on the poorly preserved specimens from Hat Creek, but the specimens from Fall River Mills,

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first thoracic leg of gravid female. 13.—Medial view of right copulatory complex of male. 14.—Clasping apparatus of male. (All figures were prepared with the aid of a camera lucida. Figs. 1-4 are drawn to the scale which accompanies Fig. 1; Figs. 9 and 10 are drawn to the scale which accompanies Fig. 9; all others are drawn to the scale which accompanies Fig. 5.)

which constitute the type series, yielded the two species of *Entocythere* previously described by one of us (Kozloff, 1955) from *P. gambelii* collected in Harney County, Oregon. The Pit River joins the Sacramento River, and this drains into San Francisco Bay. It is therefore possible that the relatively few specimens from Shasta County, collected on successive days in August, 1898, and subsequently described by Faxon (1914), do indeed represent a variant of the coastal *P. nigrescens*. But the presence on some of the specimens of ostracods otherwise known only to be associated with *P. gambelii* suggests that *fortis* may be involved systematically in some way with *P. gambelii*.

Apparently crayfishes have not been collected in the vicinity of Cassel or Fall River Mills for many years, although they have been looked for. There is a possibility that indigenous crayfishes disappeared from the streams in this region during the destructive and erosive flood of 1924, caused by the melting of one of the glaciers on Mt. Shasta, or at some other time. In any case, this note concerning the ostracods associated with *fortis* should be taken into consideration by persons who may in time review the systematic relationships of crayfishes of the *gambelii-nigrescens* group.

#### SUMMARY

*Entocythere neglecta* sp. nov., taken from museum specimens of *Pacifastacus nigrescens*, collected at San Francisco, California, is described. This species appears to be most closely related to *E. ericksoni*, commensal on *P. gambelii*, but is similar in some respects to other species of *Entocythere* described from western crayfishes.

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# The Embryology of the Swim Bladder in the Common Sucker *Catostomus commersoni* (Lacepede)

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*Catostomus commersoni*, the common sucker of North America, is a representative of the family of fishes known as the Catostomidae. Within the order Ostariophysi this family is most closely related to the cypriniform groups such as the characinids, gymnotids and particularly the cyprinids. The swim bladder is, in general, a two-chambered organ in the adult members of these groups. The posterior chamber is connected at its anterior end to the gut by means of a pneumatic duct (the physostomous condition) and to the anterior chamber by means of a constricted inter-chamber canal. The anterior chamber is surrounded by a heavy, white fibrous connective tissue *tunica externa* which is connected at its anterior end to the ear by means of the Weberian apparatus.

Stewart (1926) gave a general account of the development of this sucker. The most important part of his paper is the interesting correlation of the mouth position with the feeding habits and their changes from a cyprinid-type to the characteristic catostomid-type. As far as the swim bladder is concerned, the gross fact that it begins as a single-chambered structure and later becomes two-chambered is all of the detail available.

This study was undertaken in connection with a comparative survey of the swim bladders in adult catostomids. The origin of the anterior chamber and the peculiar "nipple"-like termination of the posterior chamber posed problems whose only solution could be arrived at by an embryological study.

*Acknowledgment.*—I wish to extend my appreciation to the following individuals whose cooperation has made this study possible: Mr. C. W. Threinen, Biologist for the Wisconsin Conservation Department who procured the specimens; Miss L. A. Burwell, technician for the Department of Anatomy of the Stritch School of Medicine who prepared the serial sections; and Mr. Charles Lindsay, Photographic Department of the Stritch School of Medicine who made the microphotographs.

## MATERIALS AND METHODS

Forty-five specimens of young *Catostomus commersoni* were serially sectioned in the three major planes (Table I). The standard length (from the tip of the snout to the base of the caudal fin) of each fish was measured with a millimeter micrometer. The specimens were sectioned at 10 microns and stained with haematoxylin.

In general, the increase in standard length can be correlated with

which constitute the type series, yielded the two species of *Entocythere* previously described by one of us (Kozloff, 1955) from *P. gambelii* collected in Harney County, Oregon. The Pit River joins the Sacramento River, and this drains into San Francisco Bay. It is therefore possible that the relatively few specimens from Shasta County, collected on successive days in August, 1898, and subsequently described by Faxon (1914), do indeed represent a variant of the coastal *P. nigrescens*. But the presence on some of the specimens of ostracods otherwise known only to be associated with *P. gambelii* suggests that *fortis* may be involved systematically in some way with *P. gambelii*.

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*Acknowledgment.*—I wish to extend my appreciation to the following individuals whose cooperation has made this study possible: Mr. C. W. Threinen, Biologist for the Wisconsin Conservation Department who procured the specimens; Miss L. A. Burwell, technician for the Department of Anatomy of the Stritch School of Medicine who prepared the serial sections; and Mr. Charles Lindsay, Photographic Department of the Stritch School of Medicine who made the microphotographs.

## MATERIALS AND METHODS

Forty-five specimens of young *Catostomus commersoni* were serially sectioned in the three major planes (Table I). The standard length (from the tip of the snout to the base of the caudal fin) of each fish was measured with a millimeter micrometer. The specimens were sectioned at 10 microns and stained with haematoxylin.

In general, the increase in standard length can be correlated with

an increase in structural complexity. In a few instances a specimen appeared developmentally to belong to a size group other than that in which the specimen actually was. In these cases structural sequence rather than size sequence takes precedence, since in this study emphasis is placed on development of structure.

#### ORIGIN AND DEVELOPMENT OF THE SWIM BLADDER

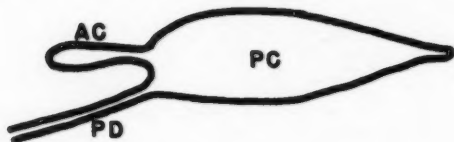
##### THE PRIMITIVE SWIM BLADDER

The initial indication of the swim bladder in this series is in the 11.2 mm size larva. A tubular structure arises from the middorsal wall of the anterior gut region and extends posteriorly between the notochord and the gut. This diverticulum expands somewhat posteriorly so as to form a single chamber broadly connected at its anterior end with the gut. This represents the primitive swim bladder with its single chamber and pneumatic duct.

A



B



C

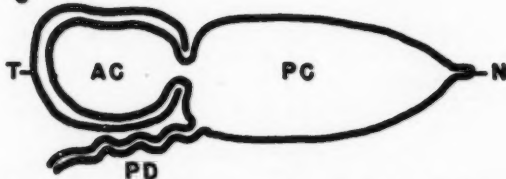


Fig. 1.—A schematic representation of the steps in the development of the swim bladder of *Catostomus commersoni*. A.—The primitive swim bladder stage. B.—The immature chambered swim bladder stage. C.—The definitive chambered swim bladder. Legend: AC, anterior chamber; N, "nipple"-like process; P, pharynx; PC, posterior chamber; PD, pneumatic duct; SB, swim bladder; and T, tunica externa.

TABLE I.—List of serial sets of *Catostomus commersoni* young used

Standard Lengths	Cross Sections	Sagittal Sections	Horizontal Sections	Totals
Just hatched	1	0	0	1
11.2 mm	2	1	1	4
12.0 - 12.4 mm	5	2	1	8
12.5 - 12.7 mm	2	3	2	7
13.0 mm	2	2	1	5
13.5 - 13.6 mm	0	2	1	3
14.0 - 14.1 mm	1	2	1	4
14.6 mm	0	1	1	2
15.0 mm	1	1	1	3
16.0 mm	3	2	0	5
17.0 mm	1	1	1	3
Total				45

The wall of the primitive swim bladder is formed of a single layer of columnar epithelium which is continuous with the columnar epithelium of the gut wall. At this time the swim bladder is already surrounded by a condensation of cellular material similar to the cellular condensation about the primitive gut (Figs. 2, 3 and 4).

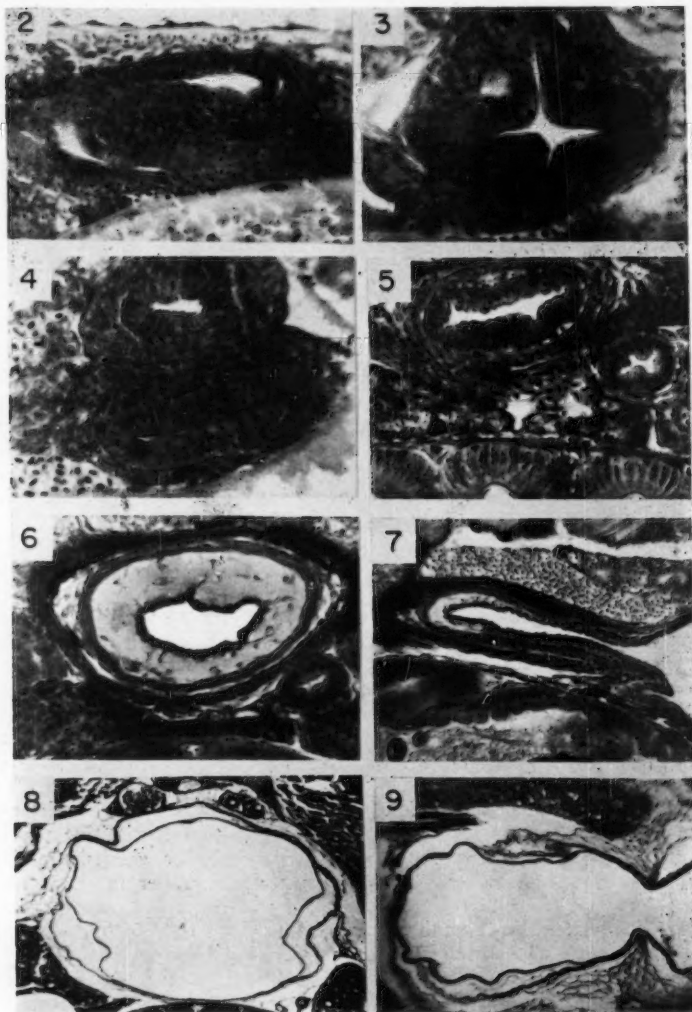
#### THE CHAMBERED SWIM BLADDER

The primitive swim bladder continues to grow caudally and its lumen expands in size. This growth is in connection with the over-all growth of the body as a whole. At an early stage (about 12.0 mm size) there arises from the anterior face of the chamber of the primitive swim bladder, dorsal to the entrance of the pneumatic duct, a tubular diverticulum quite similar in structure with the original diverticulum of the gut which produced the primitive swim bladder. This diverticulum is the beginning of the anterior chamber.

In cyto-structure the columnar epithelial cells of the anterior chamber at this early stage are more like the cells of the primitive swim bladder (Fig. 5) than those of the posterior chamber which have already become flattened (Fig. 10). The anterior chamber also becomes surrounded by concentric layers of cellular material as were the primitive swim bladder and primitive gut.

As the anterior chamber develops, its lumen becomes partially obliterated by a matrix of loose connective tissue which forms between the epithelium and the surrounding layers (Figs. 6 and 7). This matrix subsequently disappears (by 13.0 mm) and the lumen of the anterior chamber becomes quite large (Figs. 8 and 9).

The posterior chamber grows rapidly and very early the epithelial cells of its wall become flattened, leaving a large lumen (Figs. 10 and 11). The growth in length of the posterior chamber is apparently brought about by means of a semi-solid, "nipple"-like posterior ex-



Figs. 2-9.—Sections of the primitive swim bladder, anterior chamber and pneumatic duct. 2.—Sagittal section of the primitive swim bladder. 11.2 mm (X480). Note the open connection between the primitive swim bladder and the gut, which is dorsal to the gut in the mid-line. 3.—Cross section at the level where the primitive swim bladder comes off the gut. 11.2 mm (X700). 4.—Cross section at the level of the middle of the primitive swim

tension which retains the characteristics of the primitive swim bladder (Fig. 12). This extension has been noted on many definitive swim bladders of adult catostomids.

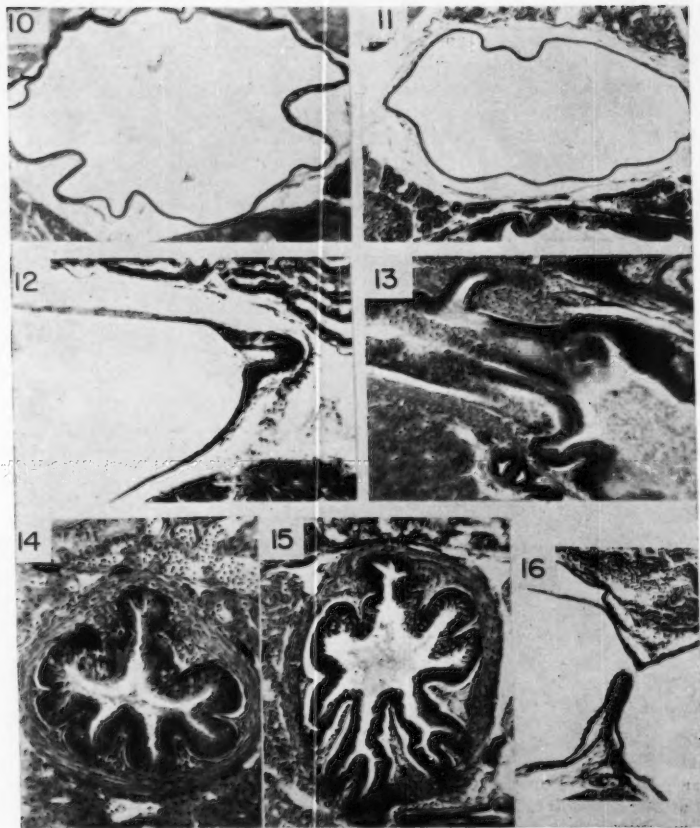
The portion of the primitive swim bladder that becomes the pneumatic duct continues to arise from the mid-dorsal wall of the anterior gut region. This region becomes the esophagus and is readily distinguished from the stomach by virtue of cyto-structural change from the "foamy" type stratified epithelium of the esophagus lining to the typical columnar epithelium of the stomach (Fig. 13). The pneumatic duct is also surrounded by the concentric cellular layers as were the primitive gut and the primitive swim bladder (Figs. 14 and 15). During the growth of the anterior chamber the pneumatic duct is displaced to the right along its length (Figs. 5, 6 and 8).

#### THE CHAMBER WALLS

The development of the chamber walls in the anterior and posterior chambers differs somewhat. In both the original epithelium layer becomes surrounded by concentric layers of cellular material as already indicated (Figs. 4 and 5). In the posterior chamber the epithelium layer and the surrounding layers become a single, composite wall (Figs. 10 and 11).

In the case of the anterior chamber a double wall is formed consisting of the *tunica externa* and the *tunica interna*. The *tunica interna* is formed of the original epithelium layer and a thin, closely applied layer of investing material (Figs. 8 and 9). The *tunica externa*

bladder. 11.2 mm (X700). The primitive swim bladder at this stage is a tubular diverticulum of the gut. The cellular components of this primitive swim bladder and of the gut are continuous. The single layer of columnar epithelium is surrounded by circular cellular condensations. 5.—Cross section of the anterior chamber and pneumatic duct. 12.0 mm (X715). Note the single layer of columnar epithelium surrounded by a condensation of other tissues very similar to the arrangement in the original primitive swim bladder. The pneumatic duct is located to the right and below the anterior chamber above the gut. 6.—Cross section of the anterior chamber and pneumatic duct. 12.4 mm (X490). Here the surrounding tissues have produced a matrix between them and the epithelium of the anterior chamber. This epithelium has become flattened to a low cuboidal type. Pigment can be seen in dorsal and lateral periphery of the anterior chamber. 7.—Sagittal section of the anterior chamber. 12.5 mm (X310). This section compares in development with that in Figure 6. The junction with the posterior chamber is broad. The junction of the pneumatic duct with the posterior chamber is ventral to that of the anterior chamber. 8.—Cross section of the anterior chamber and pneumatic duct. 16.0 mm (X130). By this stage there has been accomplished a consolidation of the matrix and of the tunics of the anterior chamber. The swim bladder also has grown considerably whereas the pneumatic duct has remained a small tubular duct below and to the right just above the gut. 9.—Horizontal section of the anterior swim bladder. 12.7 mm (X190). Note the consolidation of the connective tissues about the anterior chamber.



Figs. 10-16.—Sections of the posterior chamber and pneumatic duct. 10.—Cross section of the posterior chamber. 12.4 mm (X370). The epithelium and surrounding tissues have already consolidated to form a single layered wall to the posterior chamber. 11.—Cross section of the posterior chamber. 16.0 mm (X165). 12.—Sagittal section of the posterior chamber at its posterior end. 16.0 mm (X270). This section demonstrates the "nipple"-like terminal extension of the posterior chamber. (This condition has been frequently observed in adult swim bladders among the various Catostomidae.) 13.—Sagittal section of the esophagus—stomach junction. 12.5 mm (X270). The esophagus has a "foamy" appearing stratified epithelial lining while the stomach has a tall columnar epithelium. The pneumatic duct can be seen arising from the dorsal aspect of the esophagus. (Note also the liver diverticulum below.) 14.—Cross section of the opening of the pneumatic duct. 12.0 mm (X385). The pneumatic duct opens into the mid-dorsal line of the esophagus. The whole is surrounded by a circle of striated muscle tissue. Further caudad the



is eventually formed of two layers of heavy, white fibrous connective tissue developed entirely from the cellular material peripheral to the transient matrix between the inner and outer layers of the early anterior chamber (Figs. 6, 8 and 9). In the space between the two chambers the *tunica externa* is thickened and terminates (Fig. 16). Between the two tunics is a thin layer of loose connective tissue.

#### DISCUSSION

The swim bladder of *Catostomus commersoni* belongs to Tracy's (1911) Group 2 which includes those fishes having a sac-like, physostomous swim bladder with two chambers. Within this Group it is further restricted to those two-chambered forms having the anterior chamber derived from the posterior chamber rather than directly from the primitive swim bladder (in which case the posterior chamber is derived from a specialization of the pneumatic duct). Included in this subgroup with *Catostomus* are: the clupeoids, mormyrids and the various cypriniform ostariophysines.

The development of the swim bladder in all of the forms of this subgroup appears to be essentially the same, varying only in the details of development to arrive at the various definitive states. In all of these forms a primitive swim bladder (single-chambered, as is to be found generally in the isospondylous fishes) appears first as a dorsal diverticulum of the anterior gut region. This is followed by the formation of an anterior projection from the primitive swim bladder which subsequently becomes the anterior chamber, the pro-otic vesicles, etc., according to the particular group of fishes being studied.

Various authors have described the development of the swim bladder of cypriniform fishes, but usually as a more or less incidental item in relation to the general development of the fish. Moser (1904) and Thilo (1908) are the authors who give the most complete account of the swim bladder development in cyprinid fishes ("Karpfen"). Here the development is essentially the same as has been described for the catostomid of the present study. This includes the curious transient occlusion of the anterior chamber lumen by the inter-tunic connective tissue matrix. Thus we have another character which indicates the close relationships of the cypriniform fishes.

The role played by the transient inter-tunic matrix is unknown! Its transient nature and ground-substance-like appearance leads one

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esophagus and pneumatic duct have separate circular muscle layers. 15.—Cross section of the opening of the pneumatic duct. 16.0 mm (X190). The pneumatic duct still opens into the mid-dorsal line of the esophagus. (Ventrally the liver ducts, 2, open into this esophagus—stomach junction area.) 16.—Sagittal section of the junction between the anterior and posterior chambers of the swim bladder. 16.0 mm (X230). As in Figure 9 note how the *tunica externa* of the anterior chamber stops at the junction between the anterior and posterior chambers. This junction is somewhat dorsal in position. The pneumatic duct junction with the posterior chamber is ventral.

to consider it along with the "cardiac jelly" (Davis 1927) of the developing vertebrate heart and the "edema" of the vertebrate uterus (Krehbiel, 1937) in the early stages of pregnancy or pseudopregnancy. In all three situations one sees a transient accumulation of a matrix, restricting the lumen of the hollow organ, followed by its disappearance with the subsequent enlargement of the lumen. In all three of these hollow organs this transient matrix appears to be associated with rapid growth in the size of the lumen of the organ.

#### SUMMARY AND CONCLUSIONS

The development of the swim bladder in *Catostomus commersoni* (Lacepede) is described. The swim bladder begins as a tubular diverticulum of the middorsal aspect of the anterior gut region. This tubular process becomes the primitive swim bladder with its single chamber and pneumatic duct. A second diverticulum arises from the anterior face of the primitive swim bladder chamber, just dorsal to the opening of the pneumatic duct. This process becomes the anterior chamber of the definitive two-chambered swim bladder. The development of the anterior chamber includes a transitory phase in which the lumen is partially obliterated by a loose connective tissue matrix between the outer and inner tunics. This phenomenon has been described only for cyprinid fishes. The transient inter-tunic matrix is compared to the "cardiac jelly" of the developing vertebrate heart and to the "edema" of the vertebrate uterus in its early stages of pregnancy or pseudopregnancy. The embryology of the swim bladder of this catostomid constitutes an additional character demonstrating the common relationships of the cypriniform ostariophysine fishes.

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## Book Reviews

COMPARATIVE BIOSYSTEMATICS AND LIFE HISTORY OF THE NUTHATCHES  
*SITTA PYGMAEA* AND *SITTA PUSILLA*. By Robert A. Norris. University of  
California Publications in Zoölogy, vol. 56, no. 2, 1958, pp. 119-300. 13  
figures in text. \$3.50.

This imposing monograph is the latest in the series of incredibly detailed studies we have come to expect from Alden Miller and his colleagues and students at the Museum of Vertebrate Zoology at Berkeley. It differs in emphasis from previous papers in this series, however, in being a truly *comparative* study. The Pygmy Nuthatch of western North America and the Brown-headed Nuthatch of southeastern United States and Grand Bahama island are closely similar in appearance and in many habits, to the extent that some authors have treated them as conspecific. Norris has studied both forms intensively in the field, and also assembled 2,075 skins and 64 skeletons in order to measure inter- and intraspecific variation.

The paper opens with a chapter on the systematics of these nuthatches, based on comparisons of size and color of skins. It soon becomes apparent to the reader that *Sitta pygmaea* is one of those species, beloved of a small school of iconoclastic taxonomists, to which application of the traditional subspecies concept seems almost arbitrary. Its geographic distribution is notably discontinuous, and most of the named subspecies admitted by Norris are divisible into infraspecific populations of the type called "races" by fish taxonomists. The variation *within* some populations is illustrated by the series of *S. p. canescens*, which is restricted to the Charleston and Sheep mountains of southern Nevada. Of the 14 specimens examined from this population, three were "not distinguishable" from the subspecies *melanotis*. Norris recognizes seven subspecies of *pygmaea*, including one (*brunnescens*) named as new from Jalisco.

The Brown-headed Nuthatch, *S. pusilla*, is more nearly uniform over its more nearly continuous range. The currently-accepted Florida subspecies *caniceps* is synonymized with *pusilla* on what appear to be unassailable grounds. Only *S. p. insularis* Bond, a long-billed population restricted to Grand Bahama island, is deemed worthy of nomenclatorial recognition.

The comparison of skeletal features (chiefly of the skull) of *pygmaea* and *pusilla* is quite interesting. Because so few studies of this type have been made at the specific level among passerine birds, it is difficult to assess the significance of the differences, both clear-cut and subtle, which Norris has demonstrated between the two forms. His comparison of differences in bilacrima-width/skull-width ratio in nuthatches with differences found in certain sparrows by Linsdale is of dubious significance in view of the distant relationship and especially the dissimilar mode of life of these two passerine groups. On the other hand, Norris presents some convincing interpretations of the adaptive significance of the structural differences between the nuthatches themselves.

Nearly two-thirds of this large paper is devoted to detailed life history studies, a departure from the pattern set by previous papers in this series. Each aspect of life history (voice, territory, nest, incubation, parental care, etc.) is subdivided into convenient stages which are described separately for *pygmaea* and *pusilla*. At frequent intervals this material is summarized on comparison charts, with attention called to those aspects in which the two

to consider it along with the "cardiac jelly" (Davis 1927) of the developing vertebrate heart and the "edema" of the vertebrate uterus (Krehbiel, 1937) in the early stages of pregnancy or pseudopregnancy. In all three situations one sees a transient accumulation of a matrix, restricting the lumen of the hollow organ, followed by its disappearance with the subsequent enlargement of the lumen. In all three of these hollow organs this transient matrix appears to be associated with rapid growth in the size of the lumen of the organ.

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nuthatches differ and those in which they do not. These comparison charts represent one of the most useful features of Norris's paper, and reflect an overall care in organization of the presented material which has sometimes been lacking in earlier monographs from Berkeley.

Although Norris has actually presented two excellent life history studies during the course of his paper, the emphasis is continuously on comparison. His summary and conclusion, therefore, take up the question of conspecificity of the Pygmy and Brown-headed nuthatches. After reviewing the evidence, Norris predicts "with confidence that if the two nuthatches were to meet as contiguous or sympatric populations, they would neither hybridize successfully nor even interbreed." In view of some of the known cases of interbreeding among passerine birds, this is perhaps a bit *too* confident a prediction. Many of the individual criteria cited by Norris as specific differences could probably be matched among subspecifically-differentiated populations adapted to local ecological situations. However, this reviewer agrees that the total evidence amassed by Norris warrants the continuation of current treatment of *Sitta pygmaea* and *S. pusilla* as separate species.

Norris is to be congratulated on being able to avail himself of the liberal publication policy of the University of California Press. Few authors are able to present their findings in such detail. A total of approximately four and one-quarter pages of space, for instance, is devoted to the lists, in fine print, of exact localities for all specimens examined. Norris has been permitted to devote a full page to a table showing the timing of routines of one pair of *S. pygmaea* in excavating a nest hole ("work sessions," "recesses," and "rates of 'exits' by digging birds," all separated by sex and averaged for three different observation periods). There are no less than 36 tables of figures in all, one of which runs to six pages. In view of this elaborate treatment of the text, it is perhaps surprising to note the lack of illustrations. All but one of the 13 "figures" are maps or statistical diagrams.

It is to be hoped that this thorough study will inspire similar comparisons of other closely-related allopatric forms, although we cannot anticipate such detailed presentation of results in all instances.—KENNETH C. PARKES, Carnegie Museum, Pittsburgh, Pennsylvania.

THE FISHES OF OHIO. By Milton B. Trautman. The Ohio State University Press, Columbus, Ohio. 1957. 683 pp., 183 maps, 172 figs., 7 color pls., \$6.50.

In a preliminary portion to this excellent volume, the author, distinguished curator of vertebrate collections at Ohio State University, reviews the effects of successive glacial invasions and recessions on the drainage systems of the general Ohio area, presents a competent résumé of climatic conditions during late Wisconsin times based on recent pollen-analysis studies by various authors, and considers the probable effects of the five major climatic periods which existed prior to 1750 on the Ohio fish fauna. Trautman cites the relatively recent transformation (since 1850) of the Ohio fish fauna from one dominated by clear water species to one dominated by forms characteristic of turbid water and clayey silt bottoms. According to the author "there has been a shift from fishes of great food value to fishes unfit for human consumption." Moreover, stream fishing, which deteriorated progressively since 1900 because of increasingly unfavorable habitat, has been largely replaced by fishing from impounded waters.

A glossary of over 350 technical terms should greatly assist the sportsman



and interested layman, as well as the ichthyologist, in the identification of the Ohio fishes. The described methods of counting and measuring, for the sake of standardization, closely follow the methods of Hubbs and Lagler (1947) in *Fishes of the Great Lakes Region*. The excellent key is of the conventional dichotomous type, its use being greatly enhanced by line drawings for each of the 27 families (including the Petromyzontidae) represented.

Of special interest to the ichthyologist is a list of the natural hybrid combinations recorded for Ohio. Hybridization, according to the author, may accelerate under such environmental conditions as overcrowding, removal of isolating barriers, and presence of a considerable amount of submarginal habitat for one or both parent species.

Trautman lists six major factors affecting fish distribution and abundance in Ohio streams: 1) speed of flow, 2) physiography and types of bed rocks and soils, 3) degree and availability of soil fertility in the drainage area, 4) soil, domestic and industrial pollutants, 5) seasonal migrations and 6) population pressure from competing species.

The main body of this work (pp. 131-618) is concerned with the identification, distribution, and habitat of the 169 species and 12 additional subspecies of fish occurring in Ohio. This report is based on the author's personal examination and identification of approximately 150,000 preserved specimens (some collected as early as 1860) from over 13 institutional collections, and about 500,000 specimens collected by the author during the 1925-1950 period in over 1,250 of the roughly 1,420 Ohio townships. Although most of the fish were collected with seines and nets, hundreds were taken after "having been stunned or killed by excessive amounts of domestic, industrial and soil pollutants."

In the identification section of this report each species and subspecies, with few exceptions, is represented by a meticulous, highly detailed line drawing; in cases of marked sexual dimorphism a drawing of both sexes is included. In this section are listed general and specific characters, a description of coloration, lengths and weights of young, and the method of distinguishing from similar species.

The account for each species is accompanied by a distribution map sufficiently large so that future locality records can be easily indicated, thus showing any changes in distributional patterns of such invading species as the orange-spotted sunfish (*Lepomis humilis*) and the white perch (*Roccus americanus*). Collection localities, degree of subspecific intergradation and changes in abundance of certain species during the 1850-1950 period are all accurately indicated on these maps. Each Ohio map is accompanied by a small insert map showing the approximate present and/or original range of the species in North America.

The habitat accounts for each species embody in aggregate an enormous amount of natural history and represent the assiduously and painstakingly recorded observations of a quarter-century. The account for each form embraces data on water turbidity, pollutants, width and depth of stream during normal summer conditions, gradient, type of bottom, type of aquatic vegetation (if present), type of terrestrial vegetation along the stream margin such as a willow-pioneer weed or sycamore-elm association, and the major factors responsible for population declines or changes in distribution.

Highly authoritative and exhaustive in its treatment, clearly reflecting the dedicated energies of a great scientist, this work is not only an obligatory reference volume to the fishes of Ohio and neighboring states, it is a documentary of man's century-long use and misuse of a great natural resource. As Dr. Carl Hubbs states in his glowing foreword, *The Fishes of Ohio* represents a "disting-

guished contribution to ichthyology, ecology, hydrography, economic zoology, and good, sound natural history in general."—OLIVER S. OWEN, Mankato State College, Mankato, Minnesota.

THE SNAKES OF ONTARIO. By E. B. S. Logier. University of Toronto Press, Toronto. 1958. 104 pp., 2 color pls., 33 figs., including 16 maps. \$4.95.

A fatal snake bite, the first in Ontario in more than a century, led directly to the preparation and printing of this excellent little book. Public interest in the case, plus the hysteria that was manifest in certain quarters, encouraged the University of Toronto Press to invite E. B. Shelley Logier to undertake the assignment. They could not have selected a better man. In addition to being Canada's leading herpetologist, Logier is a thoroughly competent artist and he is skilled in writing for the public. For this is a popular book, and the opening chapter on snake lore and life histories is presented in a style that will attract even the most disinterested layman.

There also is much of value for the professional herpetologist. Two pages are devoted to each of Ontario's fourteen species of harmless snakes with information arranged under four headings—size and structure, colour (I preserve the British spelling), habits and habitat, and distribution in Ontario. Accompanying each is a fine lifelike wash drawing showing the serpent's external characteristics and pattern that are useful in making identifications. In a few instances the entire animal is depicted against a natural background. For each species there is also a map delineating the range in Ontario, plus a smaller inset map showing the range as a whole. The two venomous snakes, the fairly widespread massasauga and the timber rattlesnake (the latter now nearly extinct in Ontario), receive more lengthy attention, and there is a detailed discussion of snakebite and its proper treatment. Other features of the book include a key and many line drawings for use in identification, a brief glossary, references to other popular books on snakes, how to preserve specimens, etc. Of special interest are two very fine color plates, which, like all the other illustrations (save for two photographs), were executed by the author. One of the color plates, a garter snake lying coiled at the base of a tree, serves as the frontispiece; the other depicts with remarkable color fidelity the heads and sections of the bodies and bellies of the red-bellied, ringneck, and smooth green snakes.

All of the above may be summarized in a simple statement, *viz.*, Mr. Logier has assembled an authoritative, readable, and handsomely illustrated review of the snakes of Canada's southernmost province.—ROGER CONANT, Philadelphia Zoological Garden, Philadelphia.

## INSTRUCTIONS FOR AUTHORS

Manuscripts should be typewritten, double-spaced, with ample margins, on one side of 8½ x 11 inch paper. Tables and figures should be placed at the end of the manuscript. Each sheet should be numbered consecutively. The title and author's name along with the full mailing address of the author should be placed on the first page.

Style, arrangement, spelling, and abbreviations should conform to the usage of recent numbers of this journal. Do not underline any words except scientific names. Acknowledgments can be included in the Introduction, or may be offered as a footnote attached to the title of the article.

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